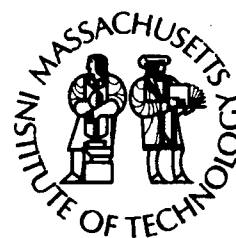# Woods Hole Oceanographic Institution

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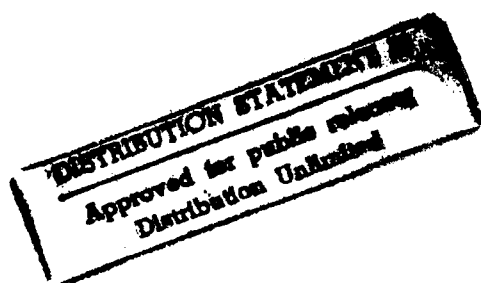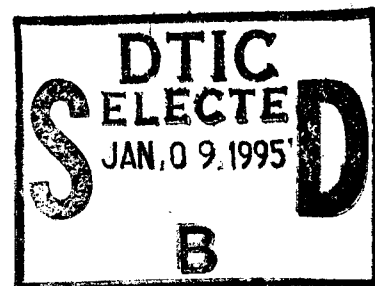### in Oceanography/
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Social Behaviour of Captive Belugas,
Delphinapterus leucas

by

Cheri Anne Recchia

February 1994

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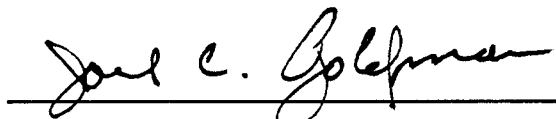Cambridge, Massachusetts 02139

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SOCIAL BEHAVIOUR OF CAPTIVE BELUGAS, *Delphinapterus leucas*

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B.Sc., University of Guelph
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Submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

at the

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For R.M.R., who made it all possible.

3

SOCIAL BEHAVIOUR OF CAPTIVE BELUGAS, *Delphinapterus leucas*

by

Cheri Anne Recchia

Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the Massachusetts Institute of Technology and the Woods Hole Oceanographic Institution.

ABSTRACT

Focal-animal sampling techniques developed for investigating social behaviour of terrestrial animals were adapted for studying captive belugas, providing quantitative descriptions of social relationships among individuals. Five groups of captive belugas were observed, allowing a cross-sectional view of sociality in groups of diverse sizes and compositions.

Inter-individual distances were used to quantify patterns of spatial association. A set of social behaviours for which actor and recipient could be identified was defined to characterize dyadic interactions. The mother-calf pair spent more time together, and interacted more often than adults. The calf maintained proximity with his mother; larger adults generally maintained proximity with smaller adults. Among adults, larger groups performed more kinds of behaviours and interacted at higher rates than smaller groups. Within dyads, the larger whale performed more aggressive behaviours and the smaller whale more submissive behaviours. Clear dominance relations existed in three groups, with larger whales dominant to smaller whales.

Vocalizations of three groups were classified subjectively, based on aural impressions and visual inspection of spectrograms, but most signals appeared graded. Statistical analyses of measured acoustic features confirmed subjective impressions that vocalizations could not be classified into discrete and homogeneous categories.

Thesis supervisor: Peter Lloyd Tyack, Associate Scientist

ACKNOWLEDGEMENTS

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CHAPTER ONE:

INTRODUCTION

1.1 Why Study Captive Belugas?

Our understanding of the social behaviour of cetaceans is extremely limited, especially in comparison to our knowledge of some terrestrial animal societies. In large part, this is due to methodological differences. Studies of the sociality of terrestrial animals have relied on long-term observations of known individuals. This type of approach allows comparison of the ways different individuals interact; relationships among individuals can be described quantitatively, and patterns elucidated. In contrast, studies of the social behaviour of cetaceans have typically involved description of the activities of groups, rather than individuals. Such studies can provide valuable information about the behavioural or activity budgets of a species, but provide little insight into the individual relationships that form the basis of a society.

The divergence in methods used in behavioural studies of terrestrial and marine species partly reflects the difficulty of observing animals that spend most of their time underwater, and thus out of view of the observer. Nonetheless, there has been increasing interest in applying terrestrial techniques to study of cetacean social behaviour. One indication of this is the increasing use of focal-animal observations by cetacean researchers. This approach consists of the observer focussing attention on a single individual rather than an entire group, and recording only interactions involving that individual (Altmann 1974). Focal-animal observations can provide detailed records of the behaviour of individuals, allowing comparison of behaviour on an individual-by-

individual basis. Focal-animal observations have recently been used with free-ranging killer whales (Rose 1992) and bottlenose dolphins (Wells 1991; Connor *et al.* 1992; Sayigh 1992; Smolker *et al.* 1992).

However, focal-animal observations are of course constrained by the visibility of the focal animals. Observations of free-ranging cetaceans are typically limited to brief glimpses obtained when the animals are at or near the water's surface. In contrast, the captive environment·can provide an opportunity for close, uninterrupted, observations, often through underwater windows. This promotes human detection of subtle interactions, and can allow observation of continuous sequences of behaviour. Additionally, detailed records often are available on the medical histories of captive animals, including records of pregnancies and births, and on the identities of poolmates since the animals were brought into captivity. Captive animals are also usually available for long-term studies, allowing examination of the temporal variability in behaviour patterns. Focal-animal studies of captive cetaceans have been conducted on bottlenose dolphins (Samuels 1988; Samuels *et al.* 1991; Östman 1991; Samuels 1992; Samuels and Gifford in prep.) and belugas (Delfour 1993).

Belugas were apparently the first cetaceans to be kept in captivity (Defran and Pryor 1988). They are currently kept at several zoos and aquaria in North America and elsewhere. This provides the prospect of studying belugas in different physical and social environments; the facilities have different pool configurations and, more importantly, groups of different sizes and compositions. Belugas also differ from bottlenose dolphins, another species commonly kept in captivity, in one important respect; they have highly

flexible necks. Bottlenose dolphins, like killer whales, porpoises, and many other odontocetes, have at least the first three cervical vertebrae fused together (Nishiwaki 1972). In contrast, beluga cervical vertebrae are typically unfused (Nishiwaki 1972), allowing a greater range of head motion. This facilitates determination by a human observer of the direction a beluga is gazing. Direction of gaze has been used by many researchers to determine the intended recipient of various animal signals (see discussion in Altmann 1967). Determination of the identities of both the sender and recipient of signals greatly facilitates assessment of signal function.

There are clearly additional factors to consider when studying social behaviour of captive animals. The captive environment places constraints on the animals' behaviour; animals are limited in their choice of associates to poolmates. Additionally, the activity budgets of captive animals are very different from wild belugas. For example, captive belugas are typically fed at regular intervals by the trainers, and they thus spend no time searching for food, and relatively little time consuming it. Care must therefore be taken in generalizing findings from the captive environment to free-ranging animals. However, it is appropriate to search for patterns of behaviour among the captive animals, and use these as starting points to launch studies of wild belugas. An understanding of beluga social behaviour is essential both for husbandry of captive animals, and effective management of free-ranging animals.

1.2 Taxonomy of Belugas

Whales, dolphins, and porpoises comprise the mammalian order Cetacea. The order is divided into two suborders: the Mysticeti, or baleen whales, and the Odontoceti,

which includes toothed whales, dolphins and porpoises. The odontocetes include the familiar bottlenose dolphin (*Tursiops truncatus*), and killer whale (*Orcinus orca*), which are both in the family Delphinidae, the dolphin family. The largest toothed whales, sperm whales (*Physter catodon*), are in the family Physeteridae. White whales or belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) currently form the family Monodontidae (Klinowska 1991).

The taxonomic classification of belugas has been the subject of some debate (Kleinenberg 1964; Gaskin 1982). Both belugas and narwhals have been excluded from the Delphinidae on the basis of skull morphology and the anatomy of the middle ear (Fraser 1966; Gaskin 1982). However, the relationship between belugas and narwhals remains somewhat controversial (Gaskin 1982). The tympano-periotic bones in the middle ears of these two genera differ in several basic characteristics, causing Kasuya (1973) to suggest placing belugas in the family Monodontidae, and narwhals in a separate family. Based on the same criteria, Kasuya (1973) also recommended transferring the Irawaddy dolphin (*Orcaella brevirostris*) from the Delphinidae to the Monodontidae. However, recent immunological and enzyme electrophoresis studies provide support for the classical taxonomic assignment of *Delphinapterus* and *Monodon* to the Monodontidae, and *Orcaella* to the Delphinidae (Lint *et al.* 1990).

There has also been some debate over whether belugas comprise a single species. Adult body size in belugas ranges from approximately 2.5 m to over 6.5 m, and varies with geographic location. The smallest belugas inhabit the White Sea and Hudson Bay, mid-sized animals are found in the eastern Canadian Arctic and the Gulf of St.

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Lawrence, and the largest animals occur off Greenland and in the Okhotsk Sea (Kleinenberg *et al.* 1964; Sergeant and Brodie 1969; but see also Doidge 1990). The variation in body size has led some researchers to postulate distinct species. However, this is generally not supported today (Kleinenberg *et al.* 1964; Sergeant and Brodie 1969; Stewart and Stewart 1989), and *Delphinapterus* is currently a monospecific genus.

1.3 General Ecology of Belugas

Belugas (*Delphinapterus leucas*, Pallas 1776) are small white whales with a circumpolar distribution in the northern hemisphere. They are principally found in shallow waters off the coasts of Canada, Alaska, Russia, Norway, and Greenland, although there is also a small relic population in the Gulf of St. Lawrence (Smith *et al.* 1990). During autumn and winter, Arctic populations form feeding aggregations near the ice edge, and their movements appear to be substantially determined by ice distribution (Seaman and Burns 1981). In the spring, these large aggregations break up into smaller groups that migrate into estuaries for the summer months.

Belugas eat a wide variety of benthic and pelagic prey, including fishes, molluscs, annelids, decapod crustaceans, and large zooplankton (Doan and Douglas 1953; Tomilin 1957; Sergeant 1962; 1973; Kleinenberg *et al.* 1964; Gurevich 1980; Seaman *et al.* 1982; Bel'kovitch and Sh'ekotov 1990). Diet varies seasonally, and with geographic location. Natural predators of belugas include polar bears (*Ursus maritimus*), killer whales, and humans. Belugas have been hunted commercially in most areas where they occur, primarily for their hide and blubber (Reeves 1990; Klinowska 1991). Except possibly in

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the former Soviet Union, commercial harvesting of belugas has largely ceased, and most belugas taken today are by local people for their own use (Klinowska 1991).

The current global population of belugas is thought to exceed 50000 animals (Braham 1984; Brodie 1989; Reeves 1990; Klinowska 1991). Population substructure is poorly understood. There are isolated year-round resident sub-populations at low latitudes, for example in the Okhotsk Sea and the St. Lawrence estuary, that form separate stocks. However, stock structure in other locations remains unclear. Debate continues over whether the large, overwintering, ice-edge groups form breeding groups, or if the smaller, summer sub-populations in river estuaries represent reproductive units (*e.g.* Finley *et al.* 1982; Braham 1984; Frost and Lowry 1990; Richard *et al.* 1990). There is some genetic evidence to support the latter hypothesis. Brennin (1992) found significant differences in the frequency distribution of mitochondrial DNA haplotypes of belugas from eastern and western Hudson Bay, and concluded that these concentrations should be regarded as separate management stocks.

1.4 Previous Work on Behaviour of Belugas

Previous research has provided a limited understanding of beluga social organization. Belugas are born brown or slate-grey, and whiten as they mature. Thus, coloration can be used as an indicator of age for immature animals. Additionally, adult males are as much as one third larger than adult females, which facilitates human discrimination of the sex of mature animals. These factors have allowed generalizations about social group size and structure (*e.g.* Sergeant 1962; Kleinenberg *et al.* 1964; Heyland 1974; Gurevich 1980; Ognetov 1981; Idle 1989; Bel'kovitch and Sh'ekotov 1990).

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Mature males appear to herd together, while females, calves, and immatures are often found together in "nursery groups" (Brodie 1989).

Belugas are highly vocal animals, and several studies have been conducted on the vocalizations of wild belugas (*e.g.* Schevill and Lawrence 1949; Ford 1977; Morgan 1979; Sjare and Smith 1986a; 1986b; Faucher 1989; Bel'kovitch and Sh'ekotov 1990), as well as captive animals (*e.g.* Fish and Mowbray 1962; Morgan 1979; Unzaga 1992). These studies have demonstrated an impressive diversity of vocalization types, including both narrow-band tonal whistles, and broad-band burst pulsed signals. Studies of the social functions of beluga vocalizations have demonstrated changes in the rates of different call types with changes in group activity (Sjare and Smith 1986b; Faucher 1989) and environmental factors, such as tidal phases (Faucher 1989). However, determination of specific functions of vocalizations has been hindered by the difficulty humans have in localizing underwater sound sources; it is thus usually impossible to determine which animal in a group made which sound (Tyack and Recchia 1991). This methodological difficulty hampers investigation of patterns of signal and response, a key approach to understanding systems of animal communication (Tyack 1991).

Studies of captive belugas have demonstrated that belugas are capable of echolocation (*e.g.* Gurevich and Evans 1976; Au *et al.* 1985; 1987; Turl *et al.* 1987; Turl and Penner 1989). Experimental investigations and comparisons with bottlenose dolphins suggest that the beluga's echolocation system is well-suited to functioning in the Arctic environment (Turl 1990). For example, belugas are better than bottlenose dolphins at detecting low amplitude signal echoes even in noisy and acoustically

reflective environments. This may reflect an adaptation to the Arctic environment, which is highly reverberant and noisy (Turl 1990).

Recently, considerable effort has been expended on trying to assess the effects of human activities on belugas. As a coastal species, they are particularly vulnerable to pollution, and high levels of organochlorine contaminants, heavy metals, and other pollutants have been found in animals from the Arctic and the St. Lawrence estuary (*e.g.* Massé *et al.* 1990; Muir *et al.* 1990; Wagemann *et al.* 1990). Other researchers have tried to evaluate the impact of ship and other industrial noise on the behaviour of belugas (*e.g.* Ford 1977; Mansfield 1983; Finley *et al.* 1990). However, there is still a need for research that will facilitate effective management of this species (Smith *et al.* 1990); this need will only increase as human demands on the marine and coastal environments continue to grow.

1.5 Comparisons with Other Odontocetes

The odontocete species in which group structure is best understood include bottlenose dolphins (*Tursiops truncatus*), sperm whales (*Physeter catodon*), and killer whales (*Orcinus orca*). Although our understanding of these species is far from complete, long-term studies of known individuals have revealed both similarities and differences in their behaviour and ecology. The patterns of association within a community of bottlenose dolphins near Sarasota, Florida, have been studied by Wells and his colleagues for over 20 years (Wells 1991). Their work has demonstrated that individually specific relationships are an important component of the social structure of these animals. The mother-calf bond may persist for many years, well beyond the one-

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to two-year period of nutritional dependence, and both males and females form stable associations with one or a few other individuals in the community (Scott *et al.* 1990). These associations appear to be based on sex, age, reproductive condition, and familial relationships (Wells 1991).

In contrast, adult female sperm whales form schools of 20-40 individuals, including calves and male and female juveniles (Best 1979). Adult and subadult males segregate by age into bachelor groups, with group size inversely correlated with average body size of group members. The mixed-sex groups are said to exhibit considerable social cohesion (Best 1979). Whitehead *et al.* (1991) studied the patterns of association of female sperm whales and their offspring off the Galapagos Islands. Each female had "constant companions" with whom she associated for periods of at least several years, as well as "casual acquaintances" who were associates for only a few days.

Perhaps the most stable relationships are those found among members of killer whale pods. Pods of killer whales in Puget Sound typically consist of 5-20 animals, including adult and juvenile males and females as well as calves (Bigg *et al.* 1990). These pods are extremely stable: in an eight-year study of 260 killer whales in 30 pods off the coast of British Columbia, no new pods were observed to form, and no permanent exchange of individuals between pods was observed. Pods within a community frequently associated and travelled together, but when these aggregations broke up, original pod compositions were maintained. Pods appear to be comprised of groups of genetically related individuals (Bigg *et al.* 1990).

Thus, long-term, close associations between individuals have been demonstrated for all three of these species. However, there are marked differences in the patterns of association. Among bottlenose dolphins, the longest-lived associations tend to be found within pairs or trios of similarly-aged males (Wells 1991). Among sperm whales, it is the adult females who have been shown to associate for periods of several years (Ohsumi 1971; Whitehead *et al.* 1991). However, both male and female killer whales maintain long-term associations, forming remarkably stable pods (Bigg *et al.* 1990). The little we know of beluga sociality thus suggests that they are more similar in this regard to bottlenose dolphins or sperm whales than killer whales. However, long-term studies of identifiable individuals are required to reveal whether belugas form stable associations with specific individuals, and, if so, whether the patterns of association resemble those described for other species.

1.6 Overview of Thesis

The objective of the research described here is to provide basic information about the social behaviour of captive belugas. Because little quantitative work has been done on beluga social relationships, it was necessary to start with very simple questions.

Chapter Two describes the selection and definition of behaviours to score. A primary goal of the thesis was to describe relations among individuals. To do this, I selected social behaviours that allowed me to determine both an actor and a recipient. This would permit comparison of the ways that specific social behaviours were used by particular individuals. Then, an appropriate behavioural sampling protocol was required

to minimize observer biases and provide good coverage of all the animals. Finally, use of the defined behaviours by individuals in each pool is described.

Chapter Three tackles the problem of operationally defining "social", based on inter-individual distance. A distance criterion is required that is practical to use and that can distinguish different relationships among the individuals. This distance criterion, once selected, can then be used to examine patterns of association between the belugas in each pool. Identification of the preferred associates of each beluga provides insight into the kinds of relationships that may exist among various individuals.

Chapter Four examines the question of whether clear agonistic dominance relations among the captive belugas can be detected. Dominance is a central feature of many animal societies, and has been demonstrated in captive bottlenose dolphins (Samuels 1988; Östman 1991; Samuels 1992).

Chapter Five describes the vocalizations produced by the captive belugas. Recorded signals are first placed into sound categories based on aural impressions and visual inspection of spectrograms. This traditional classification is then evaluated using parametric and non-parametric statistical techniques.

Finally, Chapter Six briefly summarizes the findings of Chapters Two through Five, and provides a brief discussion. Suggestions for future research are also presented.

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CHAPTER TWO:

DIRECTED SOCIAL BEHAVIOURS OF CAPTIVE BELUGAS

2.1 INTRODUCTION

Social behaviour is mediated through communication. Every act of communication requires one or more signallers and one or more intended recipients of the signal. It is often difficult to infer the addressee of an animal signal, but many visual signals are clearly directed to a specific individual by cues of gaze or body orientation. Signals with a directed visual component include body postures, gestures, and, especially in primates, facial signals. Such signals are often more accessible to the human observer than signals lacking a visual component. Determination of the individual(s) a signal is addressed to can provide much information about individual relationships. Directed signals have been reported for many species; for example, Altmann (1967) noted that most primate social signals seem to be addressed to a particular individual or individuals. Investigation of inter-individual differences in the use of directed behaviours facilitates fine-grained analysis of social organization.

Many primate species have unusually complex social organizations (Pereira and Altmann 1985; Cheney *et al.* 1987). One conspicuous feature of primate societies is that individuals may form several kinds of long-term social relationships. For example, Smuts (1985) studied long-term associations or "friendships" between individual males and females in a troop of olive baboons (*Papio cynocephalus anubis*) near Gilgil, Kenya. She found that friendships can be distinguished from ordinary male-female relationships by close and frequent spatial proximity, more frequent allo-grooming, more frequent

interactions between male friends and the female's infant, and less frequent agonistic or appeasement interactions (Smuts 1985). Smuts differentiated friendships from other types of relationships through observation of known individuals within the troop. By systematically recording who did what to whom, Smuts was able to quantify what made friendships special, because individuals behaved differently towards their friends compared to non-friends (Smuts 1985).

There are suggestions that several cetacean species may have social systems as complex as some of the non-human primates. For odontocetes in particular, there is evidence of long-term relationships between at least some individuals of several species. Killer whales (*Orcinus orca*) off Vancouver, British Columbia, travel in closed groups, or pods, whose membership may remain stable for a decade or more, despite periodic temporary joinings with other pods (Bigg *et al* 1990). Whitehead *et al* (1991) studied the association patterns of female sperm whales (*Physeter catodon*) and their dependent calves with other members of their social groups, and identified two different levels of association. Each adult female and immature animal had "constant companions" with whom they associated for periods of at least several years, as well as "casual acquaintances" who were associates for only a few days (Whitehead *et al* 1991). Wells (1991) has documented long-term, stable associations between individual bottlenose dolphins (*Tursiops truncatus*) off Sarasota, Florida. In particular, some adult male dolphins in that community have been sighted together over periods of several years (Scott *et al* 1990). However, our understanding of these relationships is limited; we know these individuals are often together, but we know relatively little of what they do together, and how that differs from the way they behave with other members of their

communities. We do not have enough information about any of these associations to compare them with baboon friendships, for example. One reason for this is that the methodologies used by marine mammal researchers and other behavioural biologists often differ.

Most studies of mammalian social behaviour rely on long-term observations of known, recognizable individuals (*e.g.* yellow baboons (*Papio cynocephalus*), Altmann 1980; red deer (*Cervus elaphus*) Clutton-Brock *et al.* 1982; capybaras (*Hydrochaeris hydrochaeris*) Herrera and Macdonald 1993; spotted hyaenas (*Crocuta crocuta*) Holekamp and Smale 1993). Sampling protocols typically involve focal-animal follows, in which usually a single individual is observed at a time. During each follow, all occurrences of an operationally-defined subset of behaviours involving the focal animal are recorded. In addition, the length of each sampling period is recorded, and the amount of time during the sample that the focal animal is actually in view is also noted (Altmann 1974). For each occurrence of the specified behaviours, the identities of the actor and the recipient, and often any other individuals within a specified distance of the focal animal, are noted. Thus patterns of behaviour among particular individuals can be examined, quantified, and compared.

In contrast, many studies of cetacean social behaviour seek to describe the activities of groups of animals. Often, "activity budgets" are generated, listing the proportion of time that the observed groups spend in a variety of behavioural states, such as travelling, socializing, or feeding (*e.g.* Hawaiian spinner dolphins *Stenella longirostris*, Norris and Dohl 1980; belugas *Delphinapterus leucas*, Sjare and Smith 1986).

The disadvantage of this type of approach is that individually-specific relationships cannot easily be detected. Two exceptions to this type of approach are studies near Sarasota, Florida, and in Shark Bay, Australia, where researchers have been able to observe interactions of free-ranging bottlenose dolphins in shallow coastal waters, by following known individuals from small boats (Wells 1991; Connor *et al.* 1992; Sayigh 1992; Smolker *et al.* 1992). Much has been learned about patterns of association among individual dolphins in these communities. Focal-animal follows have been employed in these studies, and in a few others (*e.g.* Rose 1992), but have been severely limited by the large proportion of time that the focal animals are underwater, and thus largely out of view of the observer.

The problems of conducting visual observations on animals that spend much of their time underwater are not easily solved in the wild. Thus, behavioural studies of whales and dolphins have concentrated primarily on social organization, attempting to discern the size and composition of social groups from observations of the animals when they surface to breathe. In addition, many researchers have studied surface behavioural events, which include aerial displays such as leaping from the water. However, much of the behaviour of these animals remains largely inaccessible to the surface-bound observer. Moreover, it is often difficult to determine whether surface behaviours such as leaps are directed at particular individuals, and if so, who the intended recipient is. Even the best studies of wild cetaceans yield a largely disjointed, two-dimensional view of animals that live in a three-dimensional environment. A three-dimensional perspective is best acquired through underwater observation. This is only rarely feasible, because of both the poor visibility in many areas and the high degree of mobility of the

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animals. Nonetheless, several researchers have attempted this, conducting observations while skin- or scuba-diving with the animals (*e.g.* Norris and Dohl 1980; Herzing 1991) or modifying boats to provide underwater viewing (*e.g.* Norris and Dohl 1980; Östman and Driscoll 1991). These studies have provided tantalizing glimpses of complex social interactions.

Study of captive animals can provide the opportunity for uninterrupted underwater observations of known, recognizable individuals. While the captive environment clearly affects social behaviour, and group composition in particular, it permits long-term systematic study of interactions at a level of detail rarely possible with wild marine animals. A few researchers have begun applying the techniques described above to the study of social behaviour of captive bottlenose dolphins. Östman (1991) designed a behavioural sampling program to examine sexual behaviour and aggression between two male dolphins. Samuels (1988; 1992) developed a comprehensive protocol to study the social interactions and patterns of association of a group of dolphins. Both of these studies involved continuous focal-animal observations, during which data on a carefully-defined set of behavioural events were collected. This powerful approach, which has revealed much complexity in relationships of terrestrial animals such as baboons, is proving equally productive with marine mammals.

An ideal candidate for this type of approach is the white whale or beluga. Belugas are currently kept at several aquaria in North America and elsewhere. The social organization of free-ranging belugas has been described by Ognetov (1981) and Idle (1989), among others. The behavioural states of belugas in Cunningham Inlet were

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described by Sjare and Smith (1986). Other aspects of surface behaviour, such as apparent cooperative feeding formations, have also been described (Bel'kovitch and Sh'ekotov 1990). However, we know little of the details of their social interactions or relationships, especially among adult animals. Two behavioural studies on a group of five adult belugas at the Vancouver Public Aquarium have shed some light on the social interactions of those individuals (Unzaga 1992; Delfour 1993). The purpose of this chapter is to identify and define a set of directed social behaviours that will illuminate differences in the ways that each individual behaves with other individuals. Use of these behaviours by captive belugas at several facilities with different physical and social configurations will be compared. Quantification of the way particular individuals use specific behaviours is a first step in revealing different social relationships.

2.2 METHODS

2.2.1 Sites and Study Animals

Data were collected from four aquaria: the Aquarium for Wildlife Conservation, Brooklyn, New York; the John G. Shedd Aquarium, Chicago, Illinois; the Point Defiance Zoo and Aquarium, Tacoma, Washington; and the Vancouver Public Aquarium, Vancouver, British Columbia. The ages and genders of the belugas at each facility are shown in Tables 2.1 and 2.2. Group sizes among the different facilities ranged from two to five belugas, and included a mother-calf pair. All the whales were captured from Churchill, Manitoba, in western Hudson Bay, except for the calf, who was born in captivity. Sexual maturity is thought to occur at approximately 5 years of age for females and 7-9 years for males (Stewart and Stewart 1989). All the study animals except the calf were therefore likely sexually mature, although the younger male and youngest

female in Vancouver were probably best considered adolescent (Pereira and Altmann 1985).

2.2.2 Selection of Behaviours to Score

To select a subset of directed social behaviours, I first conducted a pilot study to gain experience with the animals and with their behaviour. I observed five adult belugas at the Aquarium for Wildlife Conservation in a variety of social configurations (Table 2.1). Approximately 2320 minutes of observation were conducted during three visits to the facility. I was able to watch the same individuals in different physical and social environments, either through underwater windows or from an overhead platform. These were unstructured, or *ad libitum*, observations, during which I simply recorded what appeared to me to be salient features of the whales' social behaviour. *Ad lib.* observations tend to provide data biased towards conspicuous events and individuals, but can be of heuristic value when developing research questions and familiarity with a species (Altmann 1974). I concentrated on learning to identify individuals, and compiling a descriptive list of individual behaviours. I relied heavily on the behavioural sampling protocol developed by Samuels (1988; 1992) for study of captive bottlenose dolphins, using it as a template from which to develop a protocol suitable for belugas.

My initial list of behaviours included body postures, such as "vertical-with-head-up", and swimming positions, such as "ventral-up". However, these behaviours appeared to me usually to be undirected, and were therefore eliminated. Other apparently undirected behaviours were also excluded. These included "tail slap", in which an animal raised its tail above the surface of the water and then brought it sharply down on the

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water's surface, creating a slapping noise. Tail slaps were likely of communicative significance to the animals, but I was unable to identify possible recipients of this behaviour. "Underwater blow", in which an animal released a large volume of air from the blowhole while underwater, and "bubble stream", scored when a beluga released a series of small air bubbles from the blowhole while underwater, were eliminated for the same reason. With one exception, vocalizations were also eliminated; I could seldom tell which beluga produced a particular vocalization, let alone the intended recipient. The sole exception to this was the JAW CLAP, a sharp sound resembling a gunshot which was always accompanied by a rapid opening and closing of the jaw-clapping animal's mouth, allowing identification of both the signaller and the recipient (Table 2.3). (For clarity, behaviours I have operationally defined will be typed in small capital letters.)

To determine the apparent recipient of many behavioural acts, including JAW CLAP, I observed the direction in which the actor's rostrum was pointed, and noted the individual animal or animals in that direction. Identification of recipients was often confirmed by overt reaction to the actor's behaviour. These reactions typically involved an animal fleeing, or directing another behaviour back toward, the original actor. Scoring recipients in this way required that the actor maintain his or her head position long enough for me to look across the pool and identify the recipient. Behaviours which did not meet this requirement were excluded from my protocol. Directionality of behaviours which did not necessarily involve the actor facing another animal, such as RUB (Table 2.3), was evaluated by judging which individual was responsible for the act occurring. If both animals appeared responsible, or if I was unable to attribute the behaviour to one individual, I scored the action as "mutual". With all of the behaviours,

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I used the designation of mutual as the conservative condition; whenever I was uncertain about attributing a behaviour to a single actor, I scored the behaviour as mutual.

To interpret the behaviours, and thus the types of interactions, I next assigned each behaviour to a functional group. Functional groups were established subjectively, based on my assessment of the animals' responses to behaviours, and on temporal co-occurrence. I identified three functional groups from my observations of the New York belugas: aggressive, submissive, and affiliative. Each group contained behaviours whose function was quite clear, as well as behaviours whose function was less obvious but that tended to be closely associated with the other behaviours in the group.

To establish the category of aggressive behaviours, I began with the directed acts that were clearly aggressive: BITE, HIT, CHARGE, and CHASE (Table 2.3). These behaviours were often accompanied by HEAD JERK, MOUTH OPEN, JAW CLAP, DIRECTED LOOK, and BITE THREAT. These behaviours, whether produced alone or in combination, often provoked a FLEE response from the recipient. This provided additional evidence that the behaviours were indeed aggressive. SLOW CHARGE and CLOSED-MOUTH BITE THREAT were very similar in form to CHARGE and BITE THREAT respectively, and were also classified as aggressive. The remaining aggressive behaviours, FACE TO FACE, STARE, and MELON EXTENSION, were often produced in sequence with the more obviously aggressive behaviours.

Table 2.1. The five adult belugas at the Aquarium for Wildlife Conservation in Brooklyn, New York, observed during the pilot study. For three of the four observation periods, the whales were split into two groups housed in separate pools. N is the number of minutes animals in each pool were observed during each observation period. Each animal's location for each observation period is indicated.

Name	Sex	Age (yrs.)	3/1/91-3/6/91		4/26/91-5/1/91		5/2/91-5/9/91	7/28/91-8/2/91	
			Pool 1 N=270	Pool 2 N=60	Pool 1 N=425	Pool 2 N=140	Pool 1 N=940	Pool 1 N=235	Pool 2 N=250
Newfy	M	21	x		x		x	x	
Kathy	F	20	x		x		x		x
Natasha	F	11	x		x		x		x
Winston	M	11		x		x	x	x	
Marina	F	7		x		x	x	x	

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Table 2.2. The belugas observed for examination of frequency of occurrence of defined behaviours. Each animal was given a code indicating its sex and relative age. Thus, at a given facility, F1 was older than F2, and M1 was older than M2, except for the Point Defiance animals, who were the same age. The calf was given a special designation, C1, to clearly differentiate him from the other animals. The belugas were housed at one of four facilities: the Aquarium for Wildlife Conservation (AWC) in Brooklyn NY, the John G. Shedd Aquarium (JGSA) in Chicago IL, the Point Defiance Zoo and Aquarium (PDZA) in Point Defiance WA, and the Vancouver Public Aquarium (VPA) in Vancouver B.C. N is the total number of minutes of observation during which the specified individual was the focal animal.

Pool	Facility	Name	Code	Sex	Age (yrs.)	N (min.)	Sample dates (mo/da/yr)
1	AWC	Natasha	F1	F	13	162	6/25/93-6/28/93
		Hudson	C1	M	2	162	
2	AWC	Newfy	M1	M	23	206	1/15/93-1/19/93,
		Winston	M2	M	13	220	3/6/93-3/9/93
3	JGSA	Immiayuk	F1	F	6	80	2/2/92-2/21/92
		Puiji	F2	F	6	80	
4	PDZA	Inuk	M1	M	12	466	4/12/93-4/22/93
		Mauyak	F1	F	12	452	
		Sikku	F2	F	12	463	
5	VPA	Nanuq	M1	M	11	432	3/27/93-4/10/93
		Imaq	M2	M	7	428	
		Kavna	F1	F	23	421	
		Allua	F2	F	11	429	
		Aurora	F3	F	7	423	

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Behaviours which were clearly submissive included FLEE and FLINCH (Table 2.3). CLOSE FLEE was often used to avoid apparent attempted bites, and was also classified as submissive. LOOK AWAY and ROLL AWAY often immediately preceded FLEE, and were also produced alone in response to the milder aggressive behaviours, such as STARE. LIE PASSIVE and AVOID were most often produced immediately before or after the other submissive behaviours, although they also occurred in association with sexual behaviours. Thus they too were also placed in the submissive category.

Affiliative behaviours were those given in contexts characterized by gentle contacts between individuals, synchronized swimming behaviours, and prolonged periods of close spatial proximity, but not including sexual behaviours. RUB, CONTACT SWIM, ECHELON SWIM, and FOLLOW SWIM were categorized as affiliative, along with all non-aggressive and non-sexual CONTACT behaviours (Table 2.3).

The list of behaviours generated during observation of the adult belugas in New York required some modification to describe adequately the social activities of the remaining study animals. It was necessary to add duration and/or distance criteria to some behaviours to reduce the level of subjectivity involved in deciding whether the behaviours had occurred. These criteria reflected both practical constraints and my impressions of significance to the animals. For example, two belugas moving around in a limited space could "happen" to swim side-by-side for brief periods, but when this occurred with animals who were within 3 m of each other and persisted for 3 s or longer it appeared to indicate cooperation at some level, and was scored as an ECHELON SWIM.

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Similarly, a recipient of a STARE was more likely to react if the stare persisted for at least 3 s.

It was also necessary to add a few new behaviours to the sampling protocol to describe interactions not seen previously. For example, the belugas in Vancouver and Point Defiance engaged in sexual behaviours not seen in New York. I defined and added to the protocol the minimum number of distinct behaviours required to describe these interactions. The mother and calf in New York also necessitated the addition of new behaviours, such as those associated with nursing. These new behaviours also required the definition of two additional functional groups: sexual and calf behaviours.

The sexual category was defined to encompass all behaviours associated with apparent reproductive behaviours, such as THRUST WITH ERECTION (Table 2.3), but it is to be stressed that this label was strictly descriptive. Sexual behaviours in belugas are likely to serve many functions in addition to reproduction, as is true of many species. Other clearly sexual behaviours were THRUST (without erection), VENTRAL-TO-VENTRAL CONTACT, VENTRAL PRESENT, and VENTRAL SWIM. NODDING, PARTIAL MOUTH OPEN, and MELON RETRACTION were often produced immediately before THRUST and THRUST WITH ERECTION, and were also classified as sexual.

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Table 2.3. The directed social behaviours selected for inclusion in the behavioural sampling protocol. Subjective functional groupings are given for all behaviours except APPROACH, LEAVE, and PASS-BY, which occurred in all behavioural contexts, and thus could not be assigned to one particular functional group. A two- or three-letter code and brief description are given for each behaviour. More precise definitions are given in the text.

Functional Group	Code	Behaviour	Description
N/A	AP	APPROACH	An animal approaches to within 3 m of another.
	LV	LEAVE	An animal leaves another, increasing the inter-individual distance to more than 3 m.
	PB	PASS-BY	An animal swims past another, coming within 3 m.
Aggressive	HI	HIT	An animal hits another.
	BI	BITE	An animal bites another.
	BT	BITE THREAT	While facing another whale, an animal opens its mouth and makes a rapid lateral movement of the head parallel to and within 0.5 m of the other's body.
	CBT	CLOSED-MOUTH BITE THREAT	Same as BITE THREAT, but made with mouth closed.
	CG	CHARGE	An animal swims directly at another at full speed, traveling at least 3 m.
	SCG	SLOW CHARGE	Same as CHARGE, but at less than full speed.
	CH	CHASE	An animal chases another, with the inter-individual distance less than 3 m and the two animals traveling at least 3 m.
	JC	JAW CLAP	While facing another, an animal rapidly opens and closes its mouth while producing a short, loud sound resembling a gunshot.
	MO	MOUTH OPEN	While facing another, an animal opens its mouth fully and holds it open for at least 1 s.
	DL	DIRECTED LOOK	An animal rapidly and vigorously moves its head laterally to point its rostrum at another, often with a re-orientation of the entire body towards the other animal.

	Code	Behavior	Description
	HJ	HEAD JERK	While facing another, an animal makes a rapid and vigorous up-and-down or down-and-up motion of the head.
	FF	FACE TO FACE	While facing each other, two animals bring their heads within 1.0 m, and maintain their relative positions for at least 3 s.
	ST	STARE	While lying still in the water, an animal looks directly and intently at another for at least 3 s.
	ME	MELON EXTENSION	While facing another, an animal deforms its melon, pushing it forward (cranially) and forming it into a ball shape.
Submissive	FL	FLEE	An animal rapidly swims directly away from another, traveling at least 3 m.
	CFL	CLOSE FLEE	While within 3 m of another, an animal swims rapidly back and forth in zigzag fashion, with a path length of at least 3 m.
	HA	FLINCH	An animal rapidly lowers its head and hunches its shoulders, while turning its head to face away from another.
	LA	LOOK AWAY	An animal turns its head to face directly away from another.
	RA	ROLL AWAY	An animal rolls its body to orient its entire ventral surface directly away from another.
	AV	AVOID	An animal moves a part of its body to avoid contact with another that would otherwise have occurred.
	LP	LIE PASSIVE	In response to a TE, TR, BI, or BT, and animal ceases any swimming motions and lies still or glides through the water.
Affiliative	RB	RUB	An animal rubs another.
	CT	CONTACT	An animal touches another, but does not rub.
	CS	CONTACT SWIM	An animal touches another, and maintains contact for at least 3 s.
	ES	ECHELON SWIM	While within 3 m of another, an animal alters its swim speed and direction to swim parallel to another, and maintains this relative position for at least 3 s.

	Code	Behavior	Description
Sexual	FS	FOLLOW SWIM	A form of ECHELON SWIM in which an animal swims behind another.
	TR	THRUST	While within 3 m of another, an animal thrusts its genital region at the other whale.
	TE	THRUST WITH ERECTION	Same as THRUST, but performed with a clearly visible erect penis.
	VV	VENTRAL-TO-VENTRAL CONTACT	A particular type of CONTACT in which an animal brings its genital region into contact with another's genital region.
	VP	VENTRAL PRESENT	While within 3 m of another, an animal rolls to orient its genital region towards the other animal.
	VS	VENTRAL SWIM	A VENTRAL PRESENT that is maintained for at least 3 s.
	ND	NODDING	While facing another, an animal makes small, rapid head movements in the vertical (dorsoventral) plane.
	PMO	PARTIAL MOUTH OPEN	While facing another, an animal opens its mouth halfway or less, and maintains this position for at least 1 s.
	MR	MELON RETRACTION	While facing another, an animal deforms its melon, flattening it and moving it backwards (caudally).
Calf	LO	LOCK-ON	An animal takes one of a female's teats in its mouth and holds on for at least 3 s.
	BU	BUMPING	An animal swims parallel to and under another, and bumps the genital region by repeatedly raising and lowering its head.
	NZ	NUZZLE	A particular form of CONTACT in which an animal gently touches another with its closed or barely open mouth.
	PG	PIGGYBACK	A particular form of ECHELON SWIM in which an animal swims directly above another, with its head just behind the other's dorsal ridge.

The final category was calf behaviours. These were behaviours associated with suckling by the calf, and included LOCK-ON, BUMPING, NUZZLE, and PIGGYBACK (Table 2.3). The first two of these behaviours were integral components of suckling, while the latter two tended to immediately precede and follow nursing bouts.

The last additions to the protocol were used to indicate any breaks in the data, such as when animals were temporarily out of my view, or when I missed the beginning of a behaviour and thus could not be absolutely certain that it occurred. I attempted to count all occurrences of each behaviour. However, if a particular behaviour by an individual beluga was repeated too quickly to allow an accurate count, I indicated this in the data by adding the suffix "s" to the relevant behavioural code. Two of the behaviours, BUMPING and NODDING, occurred as rapid sequences of the same movements, which prevented accurate counts of all occurrences of each bump and each nod. For these two behaviours, bouts were scored as single occurrences. In both cases, a bout was defined as a series of individual bumping or nodding movements that were separated by less than 3 s.

2.2.3 Frequencies of Occurrence

Occurrences of the defined directed behaviours were examined in five groups of whales at four different facilities. Data were collected during brief trips to each facility (Table 2.2). The belugas were observed through underwater windows or, for the males at the Aquarium for Wildlife Conservation, from approximately 10 m above the pool. There were one or two areas in each pool where animals could not be seen.

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Fortunately, these areas were small enough that animals were completely out of view rarely, and then only briefly. A note was made whenever the focal animal was out of view, and the approximate duration of the out-of-view period was recorded.

An effort was made to complete at least one focal-animal follow on every beluga in the pool during each observation session. Observation sessions were typically conducted early in the morning, when interruptions were relatively unlikely to occur, but were also carried out at various times throughout the day. The earliest sessions were conducted at about 7:00 am, and the latest about 6:30 pm. All the study animals were housed in pools lit only by ambient light, so earlier and later observations were not possible. The length of each sample was predetermined, and was not influenced by the animals' activities. The order in which the animals in a pool were followed was determined prior to approaching the pool, to prevent the animals' activities from influencing the selection of focal animals. Individuals were followed in different orders on different days, and no individual was followed twice in a row in the event of consecutive sessions. Follows were separated by a minimum of one minute between the end of one follow and the start of the next, and averaged 10 min. in duration. Data were collected by narrating into a portable audio cassette recorder to allow uninterrupted observation. Tapes were later transcribed onto data sheets, and the data were then entered into a computer for analysis.

As a preliminary comparison of behaviours observed at the different facilities, I tallied the total number of types of behaviours observed and the total number of

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behaviours observed across all samples from each pool. For this and all subsequent analyses, instances in which accurate counts of all occurrences of a behaviour were not obtained (as indicated in the data with the "s" suffix) were treated as single occurrences. I then calculated a mean hourly rate of behaviours observed per animal per pool as follows:

$$\frac{\text{total number of behaviours observed}}{\text{number of animals in pool * minutes pool observed}} * 60.$$

This allowed a comparison of the general level of activity between the five different pools.

APPROACH, LEAVE, and PASS-BY differed from the other behaviours in two ways. First, they were the only behaviours which were defined solely by the movements of animals relative to each other. This in turn was quantified by an approach distance criterion I had selected (Chapter Three). Second, I could not easily assign them to one of my subjective functional groups. These behaviours were observed before and after all of the other behaviours, and also in the absence of any other behaviours. I reasonably could have placed them in all of the functional groups, or in none of them. For these reasons, I excluded these behaviours from all subsequent analyses. I then tallied the total number of behaviours from each facility, but excluding APPROACH, LEAVE, and PASS-BY, and recalculated the mean rates of behaviours observed as above. This allowed a comparison of the rate at which aggressive, submissive, affiliative, sexual, and calf behaviours combined were observed in each pool.

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Differences in group size and composition might be expected to influence both the types and rates of behaviours produced in a pool. To evaluate this possibility, I calculated mean rates per hour of observation for males and females in each group size of behaviours of each functional group. Acts classified as calf behaviours were excluded from this analysis because they were uncommon among the adult belugas. The mother and her dependent calf were also excluded because their behaviour was qualitatively and quantitatively different from that of the adults. For these rates, I examined data from samples in which a particular beluga was the focal animal, and then tallied the number of times that individual performed aggressive, submissive, affiliative, and sexual behaviours. These four tallies were each divided by the total number of minutes of observation that the individual was the focal animal, and then multiplied by 60 to give a mean rate per hour. The individual mean rates for each functional group were averaged over all individuals in each sex/group-size class. Six such classes were available, consisting of males and females in two-, three-, and five-member groups. All classes were represented by two or three individuals except "males in a three-member group", which was represented by a single male. Standard errors were calculated for all means.

Group size and composition may account for some differences in the behaviour of animals at different facilities, but another factor likely to be important is individual identity. If, for example, one male in a pool is dominant to another male, averaging aggressive and submissive acts across males in that pool is likely to conceal differences in behaviour that reflect an important aspect of their relationship. To examine individual differences in behaviour, I tallied the number of times each individual directed

behaviours of each functional group towards each of its poolmates during samples in which the individual was the focal animal. These tallies were divided by the total number of minutes of observation that the individual was the focal animal, and then multiplied by 60 to give a mean rate per hour. This enabled comparison of, for example, the rates at which the oldest female in Vancouver directed aggressive behaviours at the older male versus the younger male, or the rates at which she directed affiliative behaviours at the intermediate versus youngest females.

2.3 RESULTS

2.3.1 Selected Directed Behaviours

A total of 41 distinct directed behaviours were defined and scored at each facility (Table 2.3). Fourteen behaviours were subjectively classified as aggressive, seven as submissive, five as affiliative, eight as sexual, and four as calf behaviours. The remaining three behaviours, APPROACH, LEAVE, and PASS-BY, occurred in all contexts, and were placed in a separate category.

In the following descriptions, behaviours are listed in their subjective functional groups. Each group begins with the behaviours that I felt were most representative of their functional group: the behaviours for which I was most confident of my functional interpretations. Each group ends with the behaviours that were assigned to the group on the basis of their close association with the other behaviours in the group. For simplicity, each behaviour is described in terms of two individuals. However, all behaviours could and frequently did involve more than two actors and/or more than two

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recipients; the roles of all participants in occurrences of behaviours involving the focal animal were noted. Calf behaviours are described in terms of the calf's actions towards his mother, but this was not a condition for scoring the behaviour; any belugas performing the appropriate motor acts were considered as having performed the behaviour. In fact, both BUMPING and PIGGYBACK were seen, albeit very rarely, in adult belugas. Each description includes the criteria for assessing directionality of the particular behaviour, including the conditions under which the behaviour was scored as mutual. If no explicit mention is made of mutual occurrences within a description, it is because mutual occurrences of that behaviour were not observed.

Approaches, Leaves, and Pass-bys

APPROACH -- the actor swam towards the recipient, decreasing the distance between them to 3 m or less. If two animals swam toward each other, or if neither animal was clearly responsible for the approach, it was declared mutual.

LEAVE -- the actor swam away from the recipient, increasing the distance between them to more than 3 m. If two animals swam away from each other, or if neither animal was clearly responsible for the leave, it was declared mutual.

PASS-BY -- the actor swam past the recipient, coming within 3 m of the recipient, but without obviously changing swim speed or direction. No detectable interaction occurred, and the animals did not appear to even look at each other. If two animals swam past

each other, or if neither animal was clearly responsible for the pass-by, it was declared mutual.

Aggressive Behaviours

HIT -- a particular type of contact in which the actor rapidly and forcefully hit the recipient's body, resulting in a perceptible impact on the recipient. Hits often forcibly displaced the recipient's body. Hits were usually done with the tail, but also with the side of the body or the rostrum.

BITE -- a particular type of contact in which the actor opened his or her mouth fully, and bit the recipient. A bite was only scored if actor's teeth were seen to contact the body, or if a possible bite was immediately followed by the appearance of tooth marks on the recipient. Mutual bites did occur, with two face-to-face animals bringing their open mouths in contact.

BITE THREAT -- the actor opened his or her mouth fully while perpendicular to and facing the recipient, and moved his or her head laterally, making a rapid motion but without making contact. Bite threats were only scored if the actor's mouth was within 0.5 m of the recipient's body.

CLOSED-MOUTH BITE THREAT -- same motions and criteria as BITE THREAT, but with actor's mouth closed.

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CHARGE -- the actor swam at full speed directly at the recipient, traveling at least 3 m.

SLOW CHARGE -- same as CHARGE, and with actor moving rapidly but not at full speed.

CHASE -- the actor swam rapidly at the recipient, who swam rapidly away from the actor. Actor and recipient must have travelled at least 3 m while within 3 m of each other.

JAW CLAP -- the actor, while facing the recipient, rapidly opened and then closed his or her mouth, coincident with the production of a sharp sound resembling a gunshot. A mutual jaw clap was scored when two animals directed this behaviour at each other simultaneously.

MOUTH OPEN -- the actor, while facing the recipient, rapidly opened his or her mouth fully and held it open for at least 1 s. A mutual mouth open was scored when two animals directed this behaviour at each other simultaneously.

DIRECTED LOOK -- the actor rapidly swung his or her head laterally to point the rostrum at the recipient. This behaviour often involved a rapid re-orientation of the actor's whole body towards the recipient. A mutual directed look was scored when two animals directed this behaviour at each other simultaneously.

HEAD JERK -- the actor, while facing the recipient, moved his or her head quickly in the vertical plane, producing either an up-and-down or a down-and-up motion. Each up-

and-down or down-and-up was scored as a single head jerk. A mutual head jerk was scored when two animals directed this behaviour at each other simultaneously.

FACE TO FACE -- a mutual behaviour in which the actors lay facing each other, brought their rostrums within 1.0 m of each other, and maintained this position for at least 3 s.

STARE -- the actor lay still in the water, facing the recipient, and looked intently at the recipient without moving for at least 3 s.

MELON EXTENSION -- the actor, while facing the recipient, markedly changed the shape of his or her melon, forming it into a ball and pushing it forward. A mutual melon extension was scored when two animals directed this behaviour at each other simultaneously.

Submissive Behaviours

FLEE -- the actor swam rapidly and directly away from the recipient, traveling at least 3 m.

CLOSE FLEE -- the actor swam rapidly back and forth while within 3 m of the recipient, making frequent high-speed turns and with a path length of at least 3 m.

FLINCH -- the actor rapidly lowered his or her head and hunched the shoulders, while moving the rostrum to face away from the recipient.

LOOK AWAY -- the actor moved his or her head laterally so that the rostrum came to point directly away (180 degrees) from the recipient.

ROLL AWAY -- similar to look away, but the actor rolled his or her whole body away from the recipient, so that the dorsal midline was pointed toward the recipient, and the ventrum was pointed directly away from the recipient.

AVOID -- the actor moved part of his or her body such that contact with the recipient that otherwise would have occurred did not occur. A mutual avoid was scored if two animals altered their body postures to avoid contact with each other, for example by raising or lowering their pectoral flippers or arching their backs while passing close by each other.

LIE PASSIVE -- the actor ceased any swimming movements and lay still or glided. This behaviour was the scored solely as a response to a preceding THRUST, THRUST WITH ERECTION, BITE, or BITE THREAT by the recipient to the actor, and only when actor and recipient were within 3 m of each other.

Affiliative Behaviours

RUB -- an extended form of contact in which the actor rubbed part of his or her body against the recipient. This often took the form of the actor approaching the recipient, and rubbing most of the length of the body against the back or side of the recipient. The recipient sometimes facilitated the rub, for example by arching the back slightly, but

the individual whose motions resulted in the contact occurring was considered the actor. Mutual rubs were scored if both animals appeared responsible for the contact occurring, or if I was unable to attribute responsibility to one individual.

CONTACT -- the actor contacted the recipient and did not rub. Contacts could involve virtually any part of the actor's and recipient's bodies. The actor was the animal whose movements were responsible for the contact occurring. However, this judgement was often difficult to make, and contacts were frequently scored as mutual.

CONTACT SWIM -- the actor contacted the recipient and contact was maintained for at least 3 s. This usually, but not always, occurred while both animals were swimming or gliding. The directionality of this behaviour was often difficult to determine, and was frequently scored as mutual.

ECHELON SWIM -- the actor altered his or her swim pattern to swim in parallel with the recipient, maintaining relative position to the recipient for at least 3 s. This was scored only when actor and recipient were within 3 m of each other. The directionality of this behaviour was often difficult to determine, and was frequently scored as mutual.

FOLLOW SWIM -- a particular kind of echelon swim in which the actor swam behind the recipient, maintaining relative position to the recipient for at least 3 s.

Sexual Behaviours

THRUST -- the actor formed an "S" shape with his or her body, with head and genital region moved ventrally and tail moved dorsally, and moved the genital region towards the recipient. This behaviour was only scored when the actor and recipient were within 3 m of each other, and usually occurred when the two animals were swimming in parallel. A mutual thrust was scored when two animals directed this behaviour at each other simultaneously.

THRUST WITH ERECTION -- same as THRUST but scored when the actor performed the thrust with a clearly visible erect penis. A mutual thrust with erection was scored when two animals directed this behaviour towards each other simultaneously.

VENTRAL TO VENTRAL CONTACT -- a particular type of contact in which the actor brought his or her genital region into contact with the recipient's genital region. The actor was the individual whose movements caused contact to occur. However, this was often difficult to judge, and this behaviour was frequently scored as mutual.

VENTRAL PRESENT -- the actor rolled his or her body towards the recipient, so the ventral region pointed at the recipient. Ventral present was essentially the opposite of roll away, but was scored only when the actor and recipient were within 3 m of each other. A mutual ventral present occurred if two animals directed this behaviour at each other simultaneously.

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VENTRAL SWIM -- a particular type of echelon swim in which the actor maintained a ventral present towards the recipient for at least 3 s. A mutual ventral swim was scored when two animals swam in parallel with their genital regions pointed at each other for at least 3 s.

NODDING -- the actor, while facing the recipient, repeatedly and rapidly moved his or her head up and down slightly. This was one of two behaviours for which bouts, rather that all occurrences, were scored. Bouts were separated by a minimum of 3 s.

PARTIAL MOUTH OPEN -- the actor, while facing the recipient, opened his or her mouth approximately halfway, and maintained this position for at least 1 s. The partial mouth open was visually very different from the aggressive MOUTH OPEN, which comprised a full gape.

MELON RETRACTION -- the actor, while facing the recipient, deformed his or her melon backwards, resulting in a backward-slanting and flattened forehead.

Calf Behaviours

LOCK-ON -- the calf took a teat in his mouth, and held on for at least 3 s. This behaviour was also recognized by a reduction or cessation of swimming movements by the mother, and distinctive rapid short tail motions by the calf as he maintained relative position to his mother. The duration and position (left or right teat) of each lock-on were recorded when possible.

BUMPING -- the calf swam under his mother and parallel to her, repeatedly raising and lowering its head and contacting her mammary region. This was one of two behaviours for which bouts, rather than all occurrences, were counted. Bouts were separated by a minimum of 3 s.

NUZZLE -- a particular form of contact in which the calf slowly and gently brought his closed or barely-open mouth into contact with his mother's body. Nuzzles were most often directed to the mother's side, but were also occasionally directed to her face.

PIGGYBACK -- a particular form of echelon swim in which the calf swam directly above and slightly behind the mother, with his head right above her dorsal mid-line, just aft of the dorsal ridge. This behaviour was frequently accompanied by CONTACTS each time the mother fluked.

2.3.2 Frequencies of Occurrence

At none of the facilities were all of the defined behaviours observed (Table 2.4). The greatest number of types of behaviours was observed in Vancouver, and the fewest in Chicago. The overall activity level, including APPROACH, LEAVE, and PASS-BY, was highest for the mother-calf pair and lowest for the Point Defiance belugas. Activity level excluding APPROACH, LEAVE, and PASS-BY was highest for the mother-calf pair, and lowest for the two females in Chicago. The large differences in the two rates for the Chicago females and the New York males indicate that the majority of their behaviours consisted of APPROACH, LEAVE, and PASS-BY.

Table 2.4. Occurrences of defined behaviours performed by all belugas in each pool, overall, and excluding APPROACH (AP), LEAVE (LV), and PASS-BY (PB). Types is the number of types of behaviours observed. Count is the total number of occurrences of behaviours. Rate is the mean number of behaviours performed per animal per hour. N is the number of minutes of observation for each pool. Group compositions and facility codes are explained in Table 2.2.

Pool	Facility	Group Size	N (min.)	Types	Overall		Excluding AP, LV, PB	
					Count	Rate	Count	Rate
1	AWC	2	324	17	1602	148.3	1425	131.9
2	AWC	2	435	15	1061	73.2	43	0.3
3	JGSA	2	160	7	314	58.9	7	0.7
4	PDZA	3	1381	29	2118	30.7	946	13.7
5	VPA	5	2133	39	10847	61.0	4121	23.2

In general, rates of aggressive, submissive, affiliative, and sexual behaviours increased with increasing group size for adults of both sexes (Figs. 2.1a-d). In some cases, including female aggressive behaviour and male and female sexual behaviour, this appeared to be an approximately linear function. For male aggressive behaviour and male and female affiliative behaviour, rate appeared to be a non-linear function of group size. However, female submissive behaviours showed no clear increase with increasing group size, and were actually less frequent for females in five-member groups than in three-member groups.

Males generally had higher rates of behaviour than did females, particularly in three- and five-member groups (Figs. 2.1a-d). This difference was most pronounced for the aggressive and sexual behaviours (Figs. 2.1a and 2.1d). One conspicuous exception was submissive behaviours performed by females in three-member groups, which occurred at a far higher rate than the male mean (Fig. 2.1b). However, a conspicuous feature of Figures 2.1a-d is the large error bars associated with one or more of the points in each plot. There were clearly large individual variations in some of the mean rates of behaviours performed, even within a particular sex/group-size class.

Differences in individual behaviour rates were seen in both pools at the Aquarium for Wildlife Conservation (Tables 2.5a-d and 2.6a-c). The calf performed far more affiliative and calf behaviours to his mother than she directed towards him (Tables 2.5b and 2.5c). The mother performed aggressive and sexual behaviours at slightly higher rates than did the calf (Tables 2.5a and 2.5c). No submissive behaviours were

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observed from either the mother or the calf. The two males in New York performed affiliative behaviours at similar rates (Table 2.6c). However, the older male performed more aggressive behaviours than did the younger male (Table 2.6a), and the younger male performed all of the observed submissive behaviours (Table 2.6b). No sexual behaviours were observed from either of these males.

In Point Defiance, the male performed the highest rates of aggressive, affiliative, and sexual behaviours (Tables 2.7a, 2.7c, and 2.7d). For all three of these behaviour types, the majority of the behaviours were directed to one of the two females, F2. In contrast to the two females, he performed very few submissive behaviours, but received little else (Tables 2.7a-d). F2 produced submissive acts at a much higher rate than any other whale at any facility. However, the majority of these were directed towards the male, despite the relatively high rate of aggressive behaviours she received from the other female in the pool.

In Vancouver, the older male directed aggressive acts to the younger male at the highest rate of any whale at any facility (Table 2.8a). The older male also received a high rate of submissive acts, principally from the younger male (Table 2.8b). The younger male both received and performed relatively high rates of submissive behaviours (Table 2.8b). He also had the highest rates of affiliative and sexual behaviours, which in both cases were directed towards the oldest female (Tables 2.8c and 2.8d). The youngest female received relatively high rates of affiliative behaviours (Table 2.8c). Interestingly, she also received calf behaviours from the other two females. These were exclusively

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PIGGYBACK behaviours. The only other occurrence of a calf behaviour observed from an adult was a single PIGGYBACK directed by the younger male to the oldest female.

Figure 2.1a. Mean number of aggressive behaviours per hour performed by adult male and female belugas in different-sized groups. Rates shown are from a two-male group in New York, a two-female group in Chicago, a one-male, two-female group in Point Defiance, and a two-male, three-female group in Vancouver. Details of group composition and sample sizes are given in Table 2.2. Aggressive behaviours are defined in Table 2.3. See text for details of rate calculation.

Figure 2.1b. Mean number of submissive behaviours per hour performed by adult male and female belugas in different-sized groups. Rates shown are from a two-male group in New York, a two-female group in Chicago, a one-male, two-female group in Point Defiance, and a two-male, three-female group in Vancouver. Details of group composition and sample sizes are given in Table 2.2. Submissive behaviours are defined in Table 2.3. See text for details of rate calculation.

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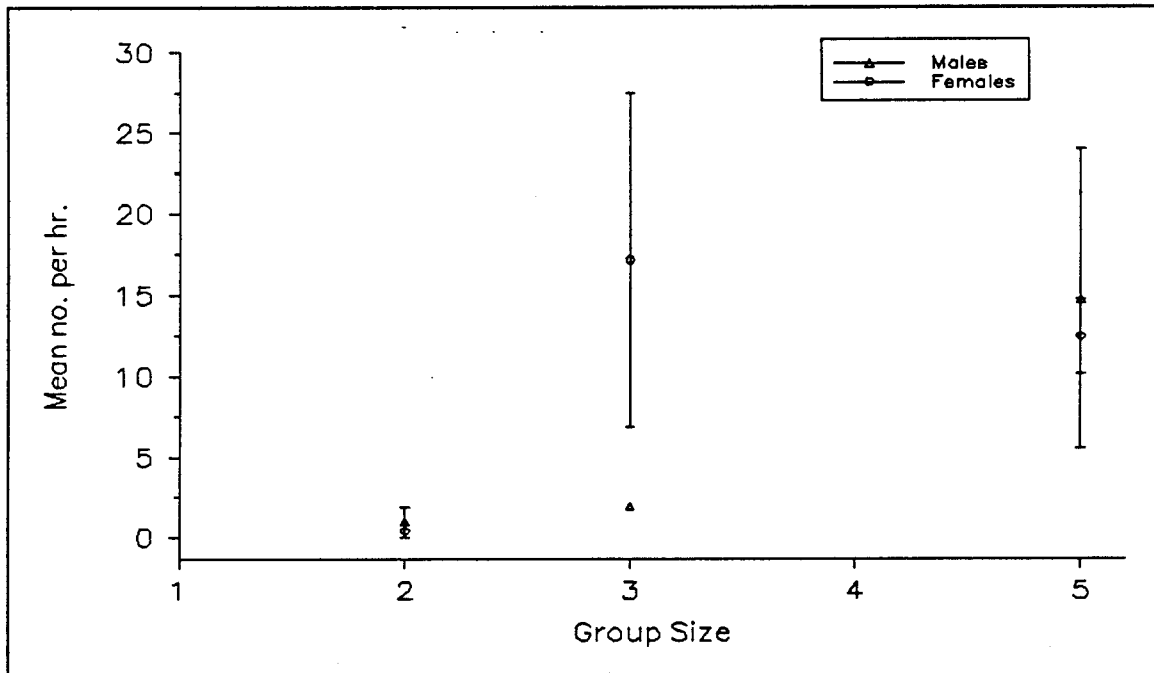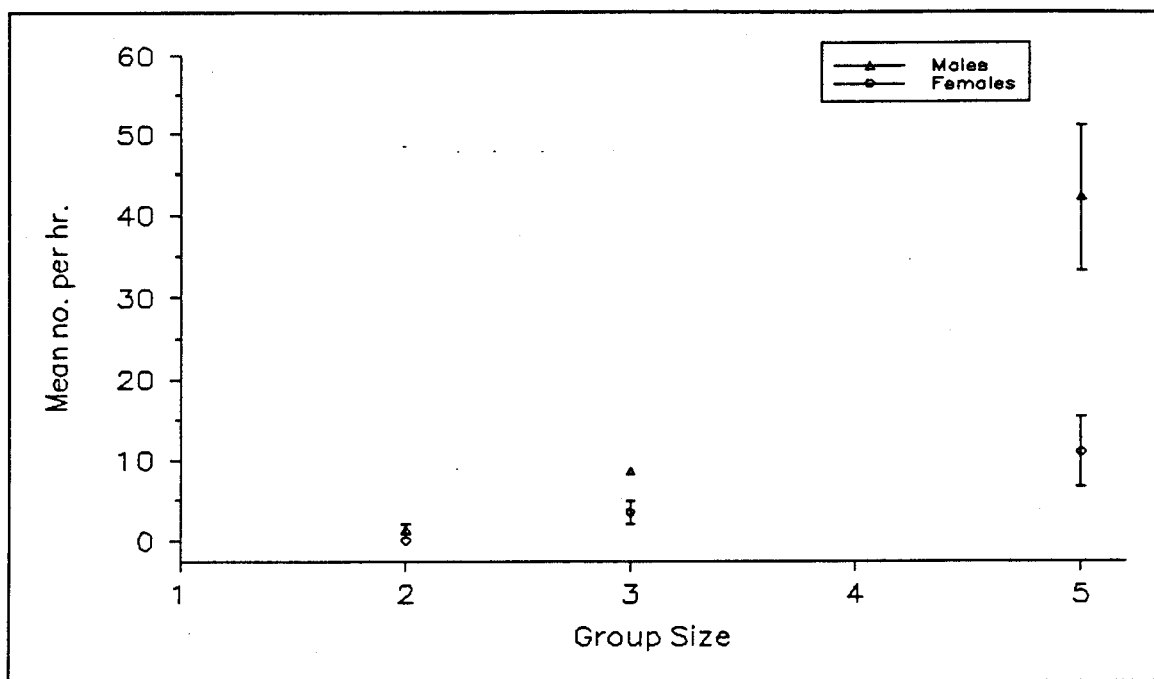
Figure 2.1c. Mean number of affiliative behaviours per hour performed by adult male and female belugas in different-sized groups. · Rates shown are from a two-male group in New York, a two-female group in Chicago, a one-male, two-female group in Point Defiance, and a two-male, three-female group in Vancouver. Details of group composition and sample sizes are given in Table 2.2. Affiliative behaviours are defined in Table 2.3. See text for details of rate calculation.

Figure 2.1d. Mean number of sexual behaviours per hour performed by adult male and female belugas in different-sized groups. Rates shown are from a two-male group in New York, a two-female group in Chicago, a one-male, two-female group in Point Defiance, and a two-male, three-female group in Vancouver. Details of group composition and sample sizes are given in Table 2.2. Sexual behaviours are defined in Table 2.3. See text for details of rate calculation.
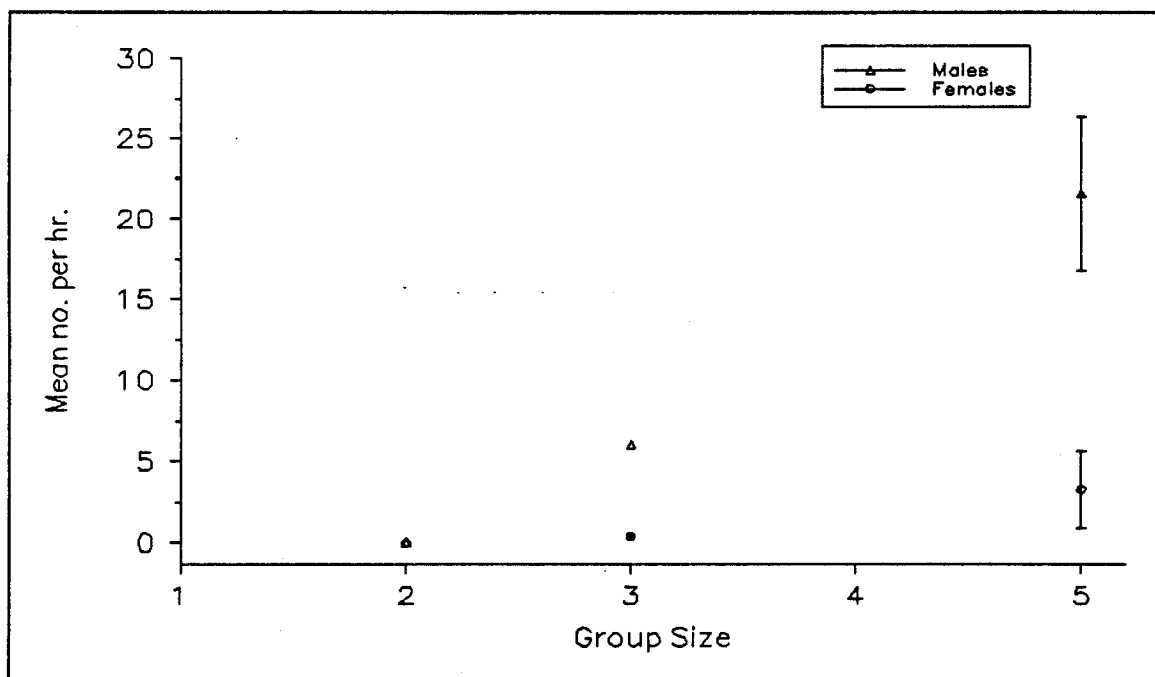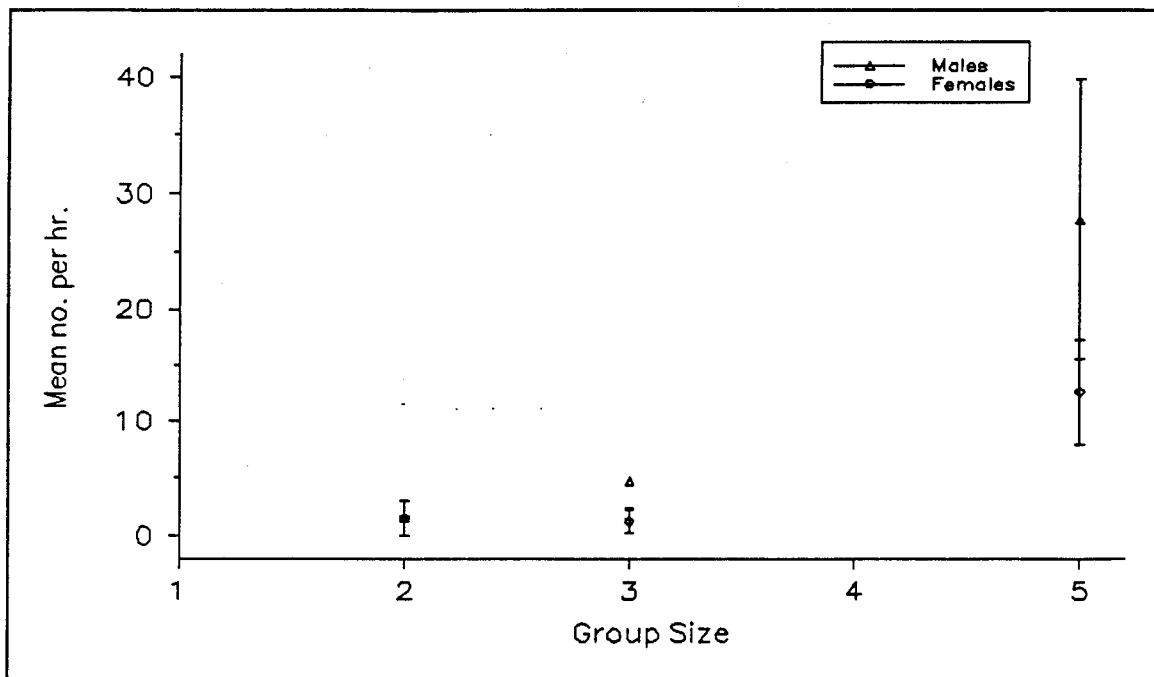
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Tables 2.5a-d. Mean rates per hour that a) aggressive, b) affiliative, c) sexual, and d) calf behaviours were directed by the mother (F1) and calf (C1) at the Aquarium for Wildlife Conservation towards each other. Animal ages and sample sizes are shown in Table 2.2. The behaviours of each type are defined in Table 2.3.

Table 2.5a. Aggressive behaviours.

	Recipient	
Actor	F1	C1
F1	---	1.1
C1	0.4	---

Table 2.5b. Affiliative behaviours.

	Recipient	
Actor	F1	C1
F1	---	51.9
C1	136.7	---

Table 2.5c. Sexual behaviours.

	Recipient	
Actor	F1	C1
F1	---	1.1
C1	0.4	---

Table 2.5d. Calf behaviours.

	Recipient	
Actor	F1	C1
F1	---	0
C1	132.6	---

Tables 2.6a-c. Mean rates per hour that a) aggressive, b) submissive, and c) affiliative behaviours were directed by the males at the Aquarium for Wildlife Conservation towards each other. Animal codes and sample sizes are shown in Table 2.2. The behaviours of each type are defined in Table 2.3.

Table 2.6a. Aggressive behaviours.

	Recipient	
Actor	M1	M2
M1	---	2.0
M2	0.8	---

Table 2.6b. Submissive behaviours.

	Recipient	
Actor	M1	M2
M1	---	0
M2	1.9	---

Table 2.6c. Affiliative behaviours.

	Recipient	
Actor	M1	M2
M1	---	1.5
M2	1.6	---

Tables 2.7a-d. Mean rates per hour that a) aggressive, b) submissive, c) affiliative and d) sexual behaviours were directed by the belugas at the Point Defiance Zoo and Aquarium towards each other. Animal codes and sample sizes are shown in Table 2.2. The behaviours of each type are defined in Table 2.3.

Table 2.7a. Aggressive behaviours.

Actor	Recipient		
	M1	F1	F2
M1	---	1.2	7.5
F1	0.1	---	4.8
F2	0.1	2.1	---

Table 2.7b. Submissive behaviours.

Actor	Recipient		
	M1	F1	F2
M1	---	0.9	0.4
F1	6.2	---	0.3
F2	20.7	7.4	---

Table 2.7c. Affiliative behaviours.

Actor	Recipient		
	M1	F1	F2
M1	---	0.1	1.9
F1	0	---	0.1
F2	0.1	0	---

Table 2.7d. Sexual behaviours.

Actor	Recipient		
	M1	F1	F2
M1	---	0.6	5.4
F1	0.3	---	0
F2	0.5	0	---

Tables 2.8a-d. Mean rates per hour that a) aggressive, b) submissive, c) affiliative and d) sexual behaviours were directed by the belugas at the Vancouver Aquarium towards each other. Animal codes and sample sizes are shown in Table 2.2. The behaviours of each type are defined in Table 2.3.

Table 2.8a. Aggressive behaviours.

Actor	Recipient				
	M1	M2	F1	F2	F3
M1	---	40.0	0.8	4.9	13.2
M2	0.3	---	0.3	24.8	1.4
F1	0	2.1	---	0.6	0.3
F2	0	9.5	0	---	4.2
F3	0	14.8	0	2.0	---

Table 2.8b. Submissive behaviours.

Actor	Recipient				
	M1	M2	F1	F2	F3
M1	---	5.0	0.4	0.1	0.1
M2	15.7	---	6.6	4.5	1.4
F1	0.9	9.8	---	0.1	0.1
F2	3.2	5.7	0.7	---	0.4
F3	5.8	9.4	0.4	2.6	---

Table 2.8c. Affiliative behaviours.

Actor	Recipient				
	M1	M2	F1	F2	F3
M1	---	5.7	2.5	0.7	2.2
M2	5.0	---	10.9[1]	3.4	1.5
F1	0.1	6.8	---	0.1[2]	3.6[3]
F2	0	1.3	0.1	---	4.3[4]
F3	0.1	0	0.3	0.7	---

Table 2.8d. Sexual behaviours.

Actor	Recipient				
	M1	M2	F1	F2	F3
M1	---	7.4	3.6	1.7	4.0
M2	4.5	---	13.2	3.4	2.4
F1	0	5.8	---	0	0
F2	0	0.8	0	---	0.3
F3	0	0.1	0	0	---

1. Includes one calf behaviour. Rate without calf behaviour is 10.8.
2. Consists of one calf behaviour only. Rate without calf behaviour is 0.
3. Includes 12 calf behaviours. Rate without calf behaviours is 1.9.
4. Includes 10 calf behaviours. Rate without calf behaviours is 2.9.

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2.4 DISCUSSION

The analyses discussed here are based on the assumption that a human observer can identify the intended recipient(s) of some signals by judging whom the actor was facing while producing the signal. Ascribing directionality to animal signals in this way is not a new technique. According to Altmann (1967, p. 331) "among primates -- and doubtless among many other animals -- facing and looking at the addressee is probably the most common means by which social messages are directed". Altmann (1967) suggests that this means of directing messages may be most efficient for animals that have both eyes on the front of the face, so other members of the group can tell who is being looked at. Although belugas have eyes on the sides of their heads, a human observer face to face with a beluga can see both of the animal's eyes simultaneously, and does receive a clear impression of being looked at. Use of apparent direction of the actor's gaze, as indicated by the orientation of the rostrum, to determine the intended recipient of a visual signal does thus seem a reasonable approach with belugas.

Many of the directed behaviours defined here have also been described by other beluga researchers. Sjare and Smith (1986) recorded jaw claps from wild belugas engaged in several types of behavioural activities, and agreed with Morgan's (1979) hypothesis that these sounds serve as attention or alerting calls in either alarm or threatening situations. In a recently-completed study of the captive Vancouver belugas, Delfour (1993) categorized their social behaviour as aggressive, intimidating, submissive, affiliative, and sexual. Although her study was completely

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independent of the work described here, many of the behaviours described are similar or identical. Delfour's (1993) aggressive and intimidating behaviours included chases, jaw claps, bites, melon extensions, stares, and mouth opens. Fleeing, and turning away from another whale, which is similar to LOOK AWAY described here, were classified as submissive behaviours. Rub, echelon-swim, and follow-swim were categorized as affiliative. Unzaga (1992), in another study of the Vancouver belugas, also postulated an aggressive function for jaw claps, which she found were more common during chases than at other times. Bartmann (1974) described aggressive behaviour by two female belugas toward a human diver in the pool. These included melon extensions, and forward thrusts with teeth showing, the latter description sounding like a CHARGE accompanied by a MOUTH OPEN.

There are also common elements from studies of other odontocete species. The majority of these are aggressive behaviours, which are the type of behaviours most commonly described in the literature. For example, Östman (1991) observed hits and bites from captive bottlenose dolphins, and categorized these as "attack" behaviours. Jaw claps and head jerks have also been observed from captive bottlenose dolphins, and are thought to be aggressive (Samuels 1988; Östman 1991), as are mouth opens (Pryor 1981; Östman 1991). Martinez and Klinghammer (1978) described an "aggressive head orientation" that they observed from a captive killer whale; from their description, I conclude that this was analogous to my DIRECTED LOOK. A similar aggressive behaviour has also been observed in captive harbour porpoises (*Phocoena phocoena*, Amundin and

Amundin 1971). The differences in form of this behaviour among the different species may be largely due to the beluga's highly flexible neck. In delphinids, including killer whales and dolphins, and in phocoenids, the porpoises, at least the first three cervical vertebrae are fused, whereas beluga cervical vertebrae are typically unfused (Nishiwaki 1972), allowing a much greater range of head motions.

Some non-aggressive behaviours have also been described. Looking away has been suggested as a submissive gesture in captive bottlenose dolphins (D. K. Caldwell and M. C. Caldwell 1972), as have flinch and flee (Samuels 1992). Ventral-to-ventral swims and ventral presents have been described as sexual behaviours for captive killer whales (Martinez and Klinghammer 1978) and harbour porpoises (Andersen and Dziedzic 1964), and are thought to serve this function (among others) in bottlenose dolphins (D. K. Caldwell and M. C. Caldwell 1972; Johnson and Norris 1986). Inter-individual rubbing and contact, and echelon swimming have been reported as affiliative behaviours for several odontocete, including wild spotted dolphins (*Stenella attenuata*, Pryor and Shallenberger 1991) and killer whales (Rose 1992), and a variety of captive species (M. C. Caldwell and D. K. Caldwell 1972; Defran and Pryor 1988).

Overall activity level differed among the groups of captive belugas in the present study. The mother-calf pair exhibited the highest rates of behaviours, both including and excluding APPROACH, LEAVE, and PASS-BY. Among adults, larger groups showed higher diversity of behaviours produced. Additionally, the two-

member groups in Chicago and New York had high activity rates when all behaviours were included, but very low rates when APPROACH, LEAVE, and PASS-BY, were excluded. Thus, these animals were sufficiently tolerant of each other to frequently pass within 3 m of one another, but did little else. In contrast, the larger groups in Point Defiance and Vancouver had much higher rates of aggressive, submissive, affiliative, and sexual behaviours. This may relate to social group size and composition in wild belugas. Idle (1989) reported that the most common group size in belugas in the Churchill River estuary was 1-2 animals. However, he does not describe the age distribution of these singles and pairs. Ognetov (1981) also reported groups of only two individuals in the White, Barents, and Kara Seas, but identified these as mothers and calves. Females and immature animals were most often seen in mixed-sex groups. Mature males were typically found either in large (mean 98 whales) all-male aggregations, or within mixed-sex groups (mean 101 whales, Ognetov 1981). Similar group sizes and compositions were reported for belugas in Cunningham Inlet, Northwest Territories, by Hay and McClung (1976). It is reasonable to expect an increase in both the frequencies of occurrence and the number of types of behaviours with an increase in social group size and diversity. This may account for the Point Defiance belugas being more active than the New York males and the Chicago females, but less active than the Vancouver belugas.

Males generally were more active than females, and produced higher rates of aggressive and sexual behaviours. However, the very small sample sizes of this

study, coupled with the large error bars for many of the mean rates for sex/group-size classes, suggest that caution in interpreting these results is warranted. Larger sample sizes would permit statistical tests of sex differences in behaviour; in the present study, there were only five matched pairs available for nonparametric comparisons. Additionally, data from more groups, or from the same individuals in groups of different sizes and compositions would allow exploration of different models of rates of social behaviours. For example, behaviour rates might increase directly as a function of group size, as a function of the total number of partners available (n-1, where n is the number of animals in the group), or might scale with the number of possible pairs in the group (n(n-1)) if dyadic interactions are an important component of beluga sociality. The data presented here do not allow testing of these alternatives. However, it is interesting that the rates of some behaviours such as female aggressive behaviour, seemed to increase linearly with group size, while others, such as male aggressive behaviours, may have scaled with n(n-1).

The mother and calf performed almost exclusively affiliative and calf behaviours. Wild beluga calves are thought to nurse for approximately two years (Brodie 1971). Hudson was slightly less than 23 months old at the time this study was conducted, and although he was eating fish every day, he still nursed frequently. Two of the most common behaviours performed by Hudson were directly associated with suckling: LOCK-ON and BUMPING. Milk was often seen when Hudson detached from the teat following a LOCK-ON, and BUMPING is

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thought to stimulate milk let-down in the mother and may also be a means for the calf to assess the fullness of the mammary glands (Cockroft and Ross 1990). The high proportion of affiliative behaviours performed by both mother and calf agrees with descriptions of the behaviour of wild beluga mothers and calves. For example, Brodie (1985, p. 560) reported that "physical contact is maintained between nursing periods, even when swimming".

The males in New York performed primarily aggressive and submissive behaviours. However, the younger male performed few aggressive behaviours, and all of the submissive acts, suggesting that he might be subordinate to the older male. The same pattern holds for the males at Vancouver. Additionally, the oldest female received submissive acts, even though she was seldom aggressive. It is possible that the older male is dominant to the younger male, and that the oldest female also holds a dominant position in the pool. The data from Point Defiance suggest that the females are subordinate to the male, and F2 may also be subordinate to F1. The relationship among the Vancouver females is less clear. The youngest female was the smallest whale in the pool, and thus may have been expected to be subordinate to all of the other animals (Chapter Three). Accordingly, she produced the highest proportion of submissive behaviours in Vancouver. However, she also received a high proportion of affiliative behaviours and was the adult animal that received most of the calf behaviours. The significance of this is unknown, and the dominance status of these animals remains uncertain.

Additionally, the present analysis relies heavily on my subjective interpretations of the functions of the various behaviours. A more quantitative analysis is desirable before conclusions are drawn about the nature of the relationships among the captive belugas. Nonetheless, the present study has provided insight into the types of behaviours performed by captive belugas in different physical and social environments. A list of operationally-defined behaviours has been compiled which will facilitate more fine-grained analyses of social relations among the captive animals. For the larger groups of belugas in Point Defiance and Vancouver, it will be possible to compare the behaviour of different pairs of animals. This study thus provides a basis for quantitative evaluation of social relationships among captive belugas. Additional, long-term studies should reveal further details, such as whether belugas form friendships analogous to those described for some baboons.

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CHAPTER THREE:

PATTERNS OF ASSOCIATION OF CAPTIVE BELUGAS

3.1 INTRODUCTION

Spatial associations between individuals constitute a fundamental aspect of sociality. Spatial proximity not only affects the physical availability of individuals to one another for social interactions (Pereira 1984), but may also reflect the nature of the social bond between animals (Altmann 1980). For example, primate researchers have long used spatial proximity as a measure of affinity between individuals (*e.g.* Kummer 1968; Smuts 1985). For a social species, several levels of spatial proximity to conspecifics may be important. Individuals may consistently arrange themselves not only into social groups, but into sub-groups as well (*e.g.* Cohen 1975). The distribution of animals into social groups may relate to ecological considerations, such as location of food patches or detection of predators, while uneven patterns of association within social groups may reflect important biological functions, such as mating and parental care. Researchers wishing to describe these different types of spatial relations must identify inter-individual distance criteria that both are biologically meaningful and practical to use. For example, many marine animals may communicate acoustically over large distances. Thus animals may be tens or even hundreds of kilometers apart and yet still form a social group. However, simultaneous monitoring of group members that are so far apart is difficult for human observers. There is therefore often a trade-off between using distances that are meaningful to the animals, and that are manageable for the observer.

White whales or belugas (*Delphinapterus leucas*), like most of the toothed whales and dolphins, are considered to be a social species. However, investigation of group size and structure is restricted primarily to brief views of animals at the surface; visual observation of animals that are underwater is extremely limited. Aggregations of hundreds or even thousands of wild belugas are reported for some areas (*e.g.* Gurevich 1980; Bruemmer 1986). Ognetov (1981) defined four types of aggregations based on group size: "singles"; "groups" of 2-10 whales; "yuros" of 11-100 whales; and "kosyaks" of more than 100 whales. Mothers and their young calves often are virtually inseparable (Brodie 1985), but little else is known of the spatial associations of individuals within groups. This is partly due to the difficulty of reliably identifying individual belugas. Individuals of several species of toothed whales are frequently identifiable by differences in pigmentation and in the size and shape of the dorsal fin (*e.g.* spinner dolphins *Stenella longirostris*, Norris and Dohl 1980; killer whales *Orcinus orca*, Bigg *et al.* 1990; bottlenose dolphins *Tursiops truncatus*, Wells *et al.* 1987). Unlike these species, belugas are virtually monochromatic (adults are usually almost entirely white) and lack dorsal fins. Moreover, males and females can be difficult to distinguish, particularly among younger animals. However, belugas are kept at several aquaria in North America and elsewhere. Study of captive animals allows virtually uninterrupted observation of known, identifiable individuals. Although captive individuals are restricted in their opportunities to choose associates, they generally have some amount of control over patterns of association within their pool. If the animals have free access to more than one pool, they have an additional level of flexibility, and associations both within and between pools can be examined.

In this chapter, I identify objective measures of association. I then use these measures to describe patterns of and consistent variability in associations between individual belugas at several aquaria that differ in physical and social configuration. This approach entails measuring the amount of time that each beluga spends in close proximity to poolmates. At facilities that house more than two belugas, the preferred associates of each individual will be identified. This information will provide insight into the types of relationships that exist among these individuals.

3.2 METHODS

3.2.1 Sites and Study Animals

Data were collected from four aquaria: the Aquarium for Wildlife Conservation, Brooklyn, New York; the John G. Shedd Aquarium, Chicago, Illinois; the Point Defiance Zoo and Aquarium, Tacoma, Washington; and the Vancouver Public Aquarium, Vancouver, British Columbia. The ages and genders of the belugas at each facility are shown in Tables 3.1 and 3.2. All the whales were captured from Churchill, Manitoba, in western Hudson Bay, except for the calf, who was born in captivity. Sexual maturity is thought to occur at approximately 5 years of age for females and 7-9 years for males (Stewart and Stewart 1989). All the study animals except the calf were therefore likely sexually mature, although the younger male and youngest female in Vancouver were probably best considered adolescents (Pereira and Altmann 1985).

Data were collected in one or more brief trips to each facility (Tables 3.1 and 3.2). This provides only a "snapshot" of the animals' behaviour; patterns of association, and behaviour in general, might change over seasons and as the animals age. The

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relationships between the individual belugas seemed to be relatively stable over the time spanned by the sampling periods at each facility. Thus initial exploration of differential associations between individuals is possible.

3.2.2 Association Distance Criterion

In watching social animals, many observers have noted that the quality of interactions differ at different inter-individual distances. For example, Smuts (1985) described special relationships, or "friendships" between some male and female olive baboons (*Papio cynocephalus anubis*) in a troop near Gilgil, Kenya. Interactions between friends differed not only in frequency, but in kind. One of the distinguishing features of these friendships was the large amount of time that the male and female spent in close spatial proximity (Smuts 1985). Thus, determination of the time that animals spend together may be an important step in characterizing relationships. Quantification of the time that animals spend together requires an operational definition of "together".

Table 3.1. The five adult belugas observed for determination of the association distance criterion. All of these belugas were housed at the Aquarium for Wildlife Conservation in Brooklyn, NY. N is the total number of observations for each individual. Observations were conducted during May 2-9, 1991.

Name	Code	Sex	Age (yrs.)	N (min.)
Newfy	F	male	21	69
Kathy	K	female	20	53
Natasha	N	female	11	58
Winston	W	male	11	34
Marina	M	female	7	10

Table 3.2. The belugas observed for analysis of patterns of association and proximity maintenance. Each animal was given a code indicating its sex and relative age. Thus, at a given facility, F1 was older than F2, and M1 was older than M2, except for the Point Defiance animals, who were the same age. The calf was given a special designation, C1, to clearly differentiate him from the other animals. The belugas were housed at one of four facilities: the Aquarium for Wildlife Conservation (AWC) in Brooklyn NY, the John G. Shedd Aquarium (JGSA) in Chicago IL, the Point Defiance Zoo and Aquarium (PDZA) in Point Defiance WA, and the Vancouver Public Aquarium (VPA) in Vancouver B.C. N is the total number of minutes of observation during which the specified individual was the focal animal.

Pool	Facility	Name	Code	Sex	Age (yrs.)	N (min.)	Sample dates (mo/da/yr)
1	AWC	Natasha	F1	F	13	178	6/25/93-6/28/93
		Hudson	C1	M	2	178	
2	AWC	Newfy	M1	M	23	234	1/15/93-1/19/93,
		Winston	M2	M	13	239	3/6/93-3/9/93
3	JGSA	Immiayuk	F1	F	6	148	2/2/92-2/21/92
		Puiji	F2	F	6	149	
4	PDZA	Inuk	M1	M	12	497	4/12/93-4/22/93
		Mauyak	F1	F	12	483	
		Sikku	F2	F	12	506	
5	VPA	Nanuq	M1	M	11	472	3/27/93-4/10/93
		Imaq	M2	M	7	469	
		Kavna	F1	F	23	460	
		Allua	F2	F	11	470	
		Aurora	F3	F	7	463	

To define when the captive belugas are together, I decided to select a single distance criterion to use in scoring animals as together, or "in association". Different relationships among the individual belugas are then discriminated by estimating the percentage of time that pairs of whales spend together. This association distance criterion should not only be relevant to the animals, perhaps reflecting their "personal space" (Altmann 1980), but must also be practical for scoring purposes. Simply measuring inter-individual distances avoids the issue of choosing a threshold value during the data collection stage, but this greatly complicates both the data collection process and the analysis. For example, Smuts (1985) used four distance categories in her study of proximity between male and female baboons. This gave four sets of proximity scores for each male-female pair. Because scores for different distance categories were not independent, and thus could not be analyzed separately, Smuts needed to develop a method to combine the scores for each pair of animals into a single measure. This required weighting the score from each distance category to reflect the area subsumed, because scores would be consistently higher in larger areas (Smuts 1985). Such an approach would be still more complicated in a captive environment, where the areas subsumed would depend in part on the animals' positions relative to pool walls. A single, biologically meaningful distance criterion for scoring spatial association is easier to use and simpler to analyze.

Several researchers of odontocete social behaviour have used a distance approximating one adult body length as the distance criterion for scoring animals as together or apart within social groups (*e.g.* Chirighin 1987; Shane 1990; Östman 1991; Rose 1992). This measure is relatively easy to score, and is intuitively appealing.

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Animals within a body length of each other can come into physical contact with little effort, which may mean that individuals are particular about who they tolerate at this distance on a regular basis or for long periods of time. Nonetheless, such an effect would presumably be a function of distance, intensifying at even shorter inter-individual distances. It is possible that a shorter distance would provide a more sensitive indicator of the nature of social relationships. However, at some point, the association distance criterion becomes so restrictive that animals are almost never scored as together, and sample sizes are too small for conclusive analyses. Thus a balance has to be found between choosing a distance criterion that is sufficiently sensitive to discriminate differences in relationships and yet provides a sufficient sample size.

At the Aquarium for Wildlife Conservation in May 1991, five adult belugas (Table 3.1) frequently had a choice of two inter-connected circular pools: a larger pool, 15.2 m in diameter by 3.3 m deep, and a smaller pool, 7.6 m in diameter by 3.0 m deep. This provided an opportunity to examine spatial associations between individuals at different levels. First, association by pool selection could be examined, to see whether animals chose which pool to occupy on the basis of which other individuals were present. Second, within the larger pool, different association distance criteria could be evaluated, to determine which one most effectively discriminated between the different types of relationships among the belugas.

Both of these approaches required measuring the proportion of time that individuals spent in particular states, such as in the smaller pool, or in association with other individuals. Instantaneous samples, in which the observer records an animal's

current activity at preselected moments in time, can provide an unbiased estimate of the proportion of time that individuals devote to each activity (Altmann 1974). If observation conditions permit, all group members can be sampled within a short time, allowing instantaneous samples to be collected on all individuals simultaneously. Such instantaneous sampling on groups is often referred to as scan sampling (Altmann 1974).

To quantify association based on pool selection, a video camera was mounted over the larger pool, and tapes were made of the animals' movements. All movements occurring in the larger pool were recorded by the camera. If individuals moved to the smaller pool, they were out of view of the camera. However, the entrance to the smaller pool was visible, so the animals entering and exiting the smaller pool could be monitored. The videotapes were reviewed and segments were chosen for analysis in which human disturbance of the whales' activity was minimal. The length of each segment analyzed was determined by human activities around the pool; samples were terminated if the animals' behaviour was clearly influenced by human behaviour, such as aquarium personnel walking around the top of the pools.

Data were collected by scan sampling of each videotape segment. Every 60 s, I recorded the locations of all five whales: larger pool or smaller pool. I then tested whether the association patterns between belugas could be explained solely on the basis of the pool preferences of the individuals, or whether animals chose pools partly on the basis of who else was there. The standard approach to this type of problem is to form a contingency table from the counts of each individual in each pool, and then use a chi-squared test to detect significant dependence (Everitt 1977). However, this test assumes

that the observations are serially independent. Because observations separated by 60 s may not meet this requirement, an alternate test for dependence between individuals (Solow *et al.* in prep.) was used.

The data consisted of five parallel sequences of observations of pool location, one for each individual. The standard test for serial dependence in binary sequences (in this case, larger pool or smaller pool) is described in Chatfield (1973). This approach essentially consists of a chi-squared test of independence in 2x2 tables of one-step transition counts, which are generated for each sequence. Significant values of a chi-squared statistic indicate first-order serial dependence in that sequence. Tests of the data sequences of three individuals revealed strong first-order serial dependence in two sequences (χ^2=10.130, p<0.001; χ^2=5.686, p=0.017), and marginal dependence in the third (χ^2=3.568, p=0.059). The other two sequences were not tested because those animals spent all, or nearly all, of their time in one pool.

Because of the serial dependence, the three sequences corresponding to the animals who spent time in both pools were modelled as first order Markov chains. To test for dependence between chains, and thus indications that these three animals chose pools partly on the basis of who else was there, the randomization approach described in Solow *et al.* (in prep.) was used. The test proceeded as follows. First, the standard chi-squared statistic for the 2x2x2 contingency table for the three sequences was calculated. This was the observed value of the chi-squared statistic. Second, as described in Solow *et al.* (in prep.), the sequences were randomized in such a way as to preserve the one-step transition counts for each sequence, thus maintaining serial dependence. Then a

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new 2x2x2 contingency table was formed from the randomized sequences, and the chi-squared statistic was re-calculated. The second step was repeated 1000 times. Significance was assessed from the proportion of the 1000 chi-squared statistics generated from the randomized sequences that exceeded the observed value. If the results of this test are significant, dependence among pairs of sequences can be tested using the same randomization procedure (Solow *et al.* in prep.).

To evaluate the effectiveness of different distance criteria in discriminating patterns of association between individuals, I measured inter-individual distances in the larger pool. Because the video camera was mounted at a slight angle to the pool and not directly overhead, the accuracy of inter-individual distance estimates varied slightly with the animals' location in the pool. Thus, instead of actual distances, I used distance categories: 0-1 m, 1-2 m, 2-3 m, and 3-4 m. The data from each video segment were collected by selecting one whale, the focal animal, and then using instantaneous sampling (Altmann 1974) to record the distance from the focal animal to each of the other whales every 60 s. Each video segment analyzed thus generated a count of the number of samples in which each of the other belugas was observed within each of the distance categories, relative to the focal animal. The identity of the focal animal for each segment was chosen prior to viewing the segment, to prevent the activities of the animals from biasing selection of focal animals. An effort was made to sample all five individuals equally.

Association as a function of distance was estimated using a pairwise association score, calculated as $(AB_A + AB_B)/(N_A + N_B)$, where AB_A is the number of observations in

which AB were within the specified distance when A was the focal animal, AB_B is the number when B was the focal animal, and N_A and N_B are the total number of observations in which A and B respectively were in the larger pool. Because all the study animals could be located every sample, this score provides an unbiased estimate of the amount of time that each pair of individuals spent together (Cairns and Schwager 1987). These calculations were made using distance criteria of 0-1 m, 0-2 m, 0-3 m, and 0-4 m to evaluate the effect of using these distances as the association criterion. The different distance categories were evaluated to determine which distance seemed to discriminate partner preferences most clearly, such that animals were not scored to be either always together or always apart. The selected association distance criterion was used in all subsequent investigation of patterns of association.

3.2.3 Time Social and Association Scores

For this and subsequent analyses, the following groups of belugas were observed: a mother-calf pair at the Aquarium for Wildlife Conservation, a pair of males, also at the Aquarium for Wildlife Conservation, a pair of females at the John G. Shedd Aquarium, a male and two females at the Point Defiance Zoo and Aquarium, and two males and three females at the Vancouver Public Aquarium (Table 3.2).

Data for all further analyses were collected live. The belugas were observed through underwater windows or, for the males at the Aquarium for Wildlife Conservation, from above the pool. To gather relatively unbiased data and approximately equal sample sizes for all individuals, focal-animal follows (Altmann 1974) were used. During each follow, instantaneous samples were collected every 60 s, and the

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social state and associates of the focal animal were recorded. The state was recorded as "social" if there were one or more individuals within the association distance criterion of the focal animal at the time of the sample, and "alone" otherwise. If the focal animal was social, the identities of the associates were recorded.

Preferred associates might vary with behavioural context. For example, an individual may have a different preferred associate when resting than when feeding, or resting animals might passively drift apart. Associations between the captive belugas were controlled during the feeding periods, but were determined by the whales at other times. To provide a coarse indicator of behavioural context, the activity state of the focal animal was also recorded during the instantaneous samples. Activity state was recorded as "swimming" if the focal animal was moving forward with tail stroking at the instant the sample was taken; anything else was identified as "resting". This had the disadvantage that any "gliding" movements were scored as resting, but eliminated the problem of trying to determine whether apparent gliding motions were due simply to water currents in the pool.

Observation sessions were typically conducted early in the morning, when interruptions were less likely to occur, but were also carried out at various times throughout the day. The earliest sessions were conducted at about 7:00 am, and the latest about 6:30 pm. Prior to beginning each observation session, an estimate was made of the time available for uninterrupted observations. In order to sample all the individuals in a pool within an observation session, the available time was divided by the number of animals in the pool to determine the appropriate length for each sample.

Thus the length of each sample was predetermined, and was not influenced by the animals' activities. The order in which the animals in a pool were followed was determined prior to approaching the pool, to prevent the animals' activities from influencing the selection of focal animals. Individuals were followed in different orders on different days, and no individual was followed twice in a row in the event of consecutive sessions. Follows were separated by a minimum of one minute between the end of one follow and the start of the next. Data were collected by narrating into a portable audio cassette recorder to allow uninterrupted observation. Tapes were later transcribed onto data sheets, and the data were then entered into a computer for analysis.

As a first measure of association, the total time spent social was calculated for each individual as the number of instantaneous samples in which the focal animal had one or more individuals within the association distance criterion divided by the total samples for each individual. This measure did not take into account the identities of any associates, but simply quantified the time that each individual spent within the association distance criterion of any other whales. This allowed comparison of patterns of association of individuals independently of the identities of associates. For example, the total time that the two-year old calf spent in association with its mother could be compared with the time that any of the adults spent in association.

To examine association preferences, association scores were calculated for all possible pairs of belugas at each facility. The association score was calculated in the same way as previously: $(AB_A + AB_B)/(N_A + N_B)$, where AB_A is the number of

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instantaneous samples in which A and B were within the association distance criterion when A was the focal animal, AB_B is the number when B was the focal animal, and N_A and N_B are the total number of instantaneous samples for A and B respectively. This provided an unbiased estimate of the percentage of time that each beluga spent with each of its poolmates.

In Vancouver and Point Defiance, where there were five and three belugas respectively, the focal animal could have more than one associate on any given sample. If animals are particular about with whom they associate, then they might be most sensitive to the identity of the animal nearest them at any particular moment. Therefore, at these facilities, an effort was made to determine which of the associates was closest to the focal animal, or the "nearest neighbour". I calculated nearest-neighbour scores using the same formula as above, but with AB_A and AB_B equal to the number of instantaneous samples in which A and B were nearest neighbours during A and B focal-animal follows respectively.

Because I expected nearest-neighbour scores to be the most sensitive measure of association for the big groups in Vancouver and Point Defiance, I examined the effect of activity state on nearest-neighbour scores. Accordingly, nearest-neighbour scores were recalculated separately for samples in which the focal animal was resting and swimming. This enabled comparison of overall nearest-neighbour scores with those for resting animals and for swimming animals.

3.2.4 Maintenance of Proximity

The members of a pair can play very different roles in determining their proximity to each other. For example, a relationship in which one individual always approaches and the other always leaves differs from one in which approaches and leaves are balanced. Hinde *et al.* (*e.g.* Hinde and Spencer-Booth 1967; Hinde and Atkinson 1970) have argued convincingly for the importance of determining the role of each member of a pair in maintaining spatial association. To assess these roles, they developed a proximity maintenance index, calculated as follows:

$$(AP_A/(AP_A + AP_B)) - (LV_A/(LV_A + LV_B)),$$

where AP_A and AP_B and LV_A and LV_B are the numbers of approaches and leaves by individuals A and B to each other. The absolute value of this index represents the asymmetry in the contributions of each member of a pair to the maintenance of spatial proximity. When the value of this index is positive, individual A is primarily responsible for maintaining proximity within the dyad; when it is negative, individual B plays the larger role (Hinde and Atkinson 1970). The maximal value of this index is +1 or -1, which obtains when one of the individuals does all of the approaching, and none of the leaving. This proximity maintenance index is also insensitive to overall differences in activity level because it depends on the proportion of approaches and leaves by individual A, rather than simply the totals. Thus, differences in the rate of approaching and leaving do not affect the value of the index.

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To calculate this index, all approaches and leaves involving the focal animal were scored concomitantly with the instantaneous samples. An approach was scored whenever the shortest distance between the focal animal and another beluga decreased to less than the association distance criterion, and a leave was scored when animals which had been together separated beyond the distance criterion. Whenever possible, the individual responsible for the approach or leave was noted. If more than one animal was responsible for the approach or leave, or if I was unable to determine who was responsible, the event was scored as "mutual", and was not included in the calculation of the proximity maintenance index.

Approaches and leaves for each pair of belugas were tallied across all observation sessions, independently of the identity of the focal animal. The proximity maintenance index can be calculated by using the approaches and leaves of either individual in the numerators. For consistency, I calculated all indices using the approaches and leaves of the male in the numerators. For same-sex pairs, I used the movements of the older animal to determine the index.

3.3 RESULTS

3.3.1 Association by Pools and Association Distance Criterion

Videotapes of the five adult belugas at the Aquarium for Wildlife Conservation were made over seven days in May, 1991. Video segments from three days were analyzed, yielding a total of 18 focal-animal follows comprising 224 minutes of observation (Table 3.1). Individual follows ranged in length from 5-25 minutes. More follows were conducted on the three older whales than the two younger animals, who

were less active and more difficult to distinguish in the videotapes. During the first 14 follows, comprising 176 minutes of observation, the belugas had access to both the larger and smaller pools. For the remaining follows, the animals were limited to the larger pool.

The two older females, Kathy and Natasha, showed clear preferences for the smaller pool, occupying it for 74% and 69% respectively of the total instantaneous samples in which animals had a choice of pools. In contrast, the young female, Marina, was in the smaller pool only 3% of the time, and the young male, Winston, was never seen in the smaller pool. The older male, Newfy, spent approximately equal time in both pools. However, pool preferences alone could not explain the animals' distribution. The sequences of pool location for Newfy, Kathy, and Natasha were significantly dependent ($\chi^2=36.999, p<0.001$). Tests for dependence between pairs of sequences revealed significant dependence between Newfy and Natasha ($\chi^2=5.47, p=0.034$) and Kathy and Natasha ($\chi^2=24.76, p<0.001$), but not between Newfy and Kathy ($\chi^2=0.19, p=0.248$). Thus, examination of groupings by pool does provide evidence of preferred associates for some of the whales. However, a more sensitive measure is clearly required to discriminate differences among the remaining pairs.

The different distance criteria resulted in different patterns of association. If two animals were considered to be together only when they were within 1 m of each other, the belugas were very seldom together (Table 3.3), only 10 of a total of 120 samples, or 8% of the time. However, if the distance criterion was increased to 2 m, animals were associated during 42, or 35% of the total samples. Using this distance criterion, the

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associations among Newfy, Kathy, and Natasha were the closest of the group. Increasing the association distance criterion to 3 m further increased the number of samples in which animals were together to 64, or 53%. The associations among Newfy, Kathy, and Natasha were still clearly the closest, and the association score for Winston and Marina was greater than zero for the first time. This pattern conformed more closely to subjective impressions and trainers' reports that the three older animals tended to associate together, while the younger animals tended to spend more of their time alone, or occasionally with each other. However, increasing the association distance criterion to 4 m had a dramatic impact on this pattern. The number of samples in which belugas were together jumped to 100, or 83% of the total. Additionally, associations between all of the individuals were high, and thus the effectiveness of the measure in discriminating different levels of association among pairs was reduced.

In light of these findings, an association distance criterion of 3 m was used for the remainder of the study. This distance was approximately equal to the lengths of the adult females, but slightly less than the adult males. Any individuals within 3 m of each other were considered to be together. This distance was relatively easy to estimate because the animals themselves could be used as a reference. Additionally, approximate pool dimensions were known for each facility, and these were used to help mitigate the effects of different perspectives on distance estimates. To facilitate comparison of behavior of belugas at different facilities, the same distance criterion of 3 m was used for each group of whales studied.

Table 3.3. Association patterns of five adult belugas in the larger of two inter-connected pools at the Aquarium for Wildlife Conservation in Brooklyn, NY. Percentages (totals) of instantaneous samples in which each beluga was within 1 m, 2 m, 3 m, and 4 m of each other beluga are shown. Two of the whales, Marina and Winston, could not be distinguished in 6 samples, thus their values are presented as ranges; if Marina's true value is high, Winston's is low. N = total number of samples that each pair was in the larger pool.

Pair of belugas	N	1 m	2 m	3 m	4 m
Newfy & Kathy	53	0	26.4 (14)	41.5 (22)	52.8 (28)
Newfy & Natasha	60	5.0 (3)	25.0 (15)	33.3 (20)	46.7 (28)
Newfy & Marina	47	0-8.5 (0-4)	2.1-10.6 (1-5)	2.1-12.8 (1-6)	6.4-17.0 (3-8)
Newfy & Winston	71	1.4-7.0 (1-5)	1.4-7.0 (1-5)	1.4-8.5 (1-6)	2.8-9.9 (2-7)
Kathy & Natasha	39	6.7 (4)	15.4 (6)	28.2 (11)	41.0 (16)
Kathy & Marina	26	0	0	0	3.8 (1)
Kathy & Winston	50	0	0	2.0 (1)	4.0 (2)
Natasha & Marina	33	0	3.0 (1)	3.0 (1)	6.1 (2)
Natasha & Winston	57	0	0	1.8 (1)	8.8 (5)
Marina & Winston	44	0	0	2.3 (1)	18.2 (8)

3.3.2 Time Social and Association Scores

The data used in this analysis were collected during research trips made to each facility (Table 3.2). All data were collected live during observation sessions. Focal-animal follows were usually 10 minutes long, or longer if time permitted. It was not always possible to observe all animals within a session because of occasional interruptions, such as unscheduled feedings or other events. For a variety of reasons, it was not possible to gather equal sample sizes for each of the five groups of whales studied at the four different facilities. However, similar sample sizes were gathered for all individuals in each group.

The individual whales that spent the most time social, or within 3 m of one or more other animals, were the mother and calf in New York (Fig. 3.1). The two males at New York spent the least time social. The females and males at the other facilities all ranged between these two extremes. There were no obvious patterns by age or gender.

The mother and calf spent much more time together than any other pair of belugas observed (Fig. 3.2a). The two Point Defiance females spent the least time together. At Vancouver, associations among mixed-sex pairs were most frequent for those involving the oldest female, intermediate for the middle female, and lowest for the youngest female. In fact, the oldest female spent more time together with the two Vancouver males than did any other pair of animals except the mother and calf. Otherwise, however, there were no clear-cut patterns by age or gender.

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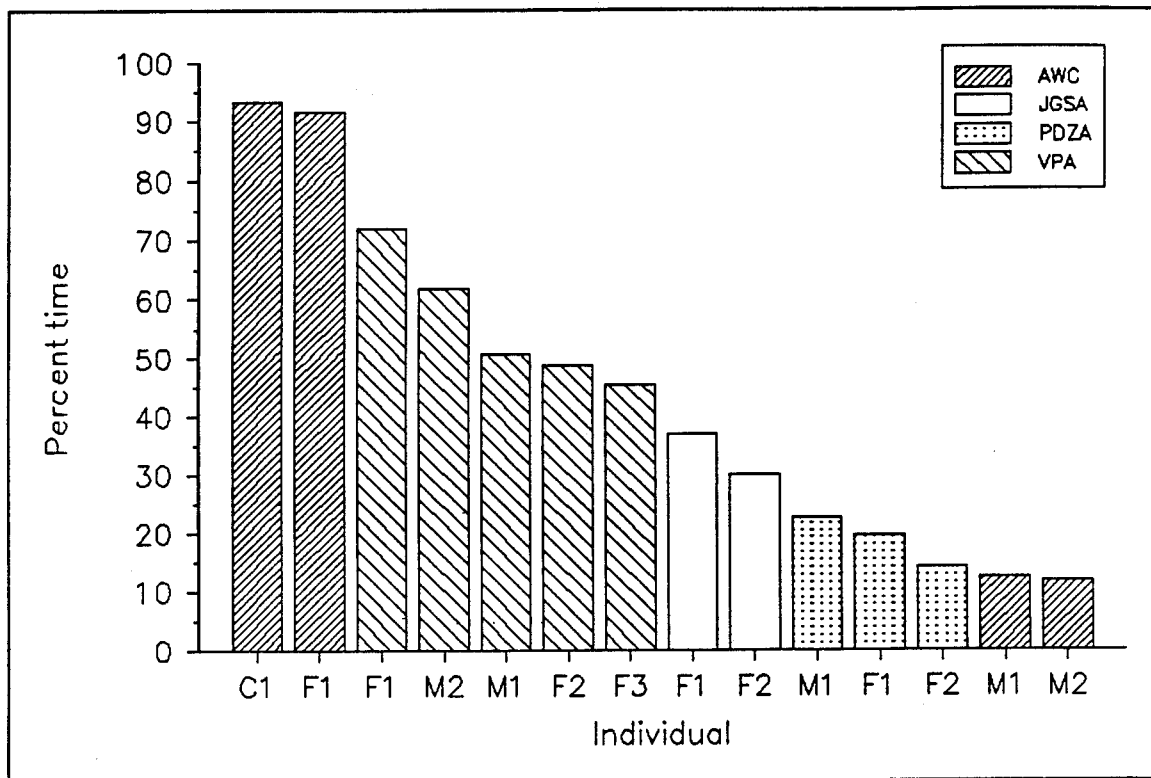
Figure 3.1. Total time that each beluga spent within 3 m of one or more other individuals, expressed as a percentage of the total time observed. Bars are arranged in descending order. Animal codes and sample sizes are given in Table 3.2. All animals at each facility are shown. Facilities are: Aquarium for Wildlife Conservation (AWC), Brooklyn, NY; John G. Shedd Aquarium (JGSA), Chicago, IL; Point Defiance Zoo and Aquarium (PDZA), Tacoma, WA; and Vancouver Public Aquarium (VPA), Vancouver, British Columbia.

As discussed earlier, nearest-neighbour scores were predicted to be the most sensitive indicator of preferred associates for the Vancouver and Point Defiance belugas, each of which had a choice of four and two associates respectively. However, at Point Defiance, all three whales were seldom together. Thus, the results from association scores (Fig. 3.2a) and nearest-neighbour scores (Fig. 3.2b) were virtually identical; by both measures, the females preferred being with the male to being with each other. However, in Vancouver, three or more animals were frequently together, and the

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difference between these two measures are very different for some of the pairs. For example, the two males were together nearly 28% of the time (Fig. 3.2a), but were each other's nearest neighbour only 15% of the time (Fig. 3.2b). In fact, these two males were often simultaneously courting the oldest female, and often swam on either side of her. Thus, although they were often in association, they were much less likely to be each other's nearest neighbour. Accordingly, the oldest female's closest associates were the two males, and she spent more of her time with them than with any other individuals, but preferred the younger male to the older male. By this measure, the preferred associate of all the Vancouver belugas was the oldest female.

Activity state did affect choice of nearest neighbour for some individuals (Fig. 3.3). For example, the male at Point Defiance preferred to rest closest to one of the females, but was more often closest to the other female when the animals were swimming. The largest effect of activity state was on the association between the oldest female and the younger male at Vancouver; when swimming, these two spent more time closest to each other than did any other animals, but they spent much less time together when resting. In fact, five of the six male-female pairs at Vancouver were closest more often when swimming than when resting. This was also true of the male-male dyad, but two of the three female-female pairs spent more time as nearest neighbours when resting. All four of the Vancouver belugas preferred to be closest to the oldest female when resting, but this was true only for the males when animals were swimming.

3.3.3 Maintenance of Proximity

The strongest asymmetry in proximity maintenance among the pairs was between the male and one of the females at Point Defiance (Fig. 3.4). The high positive value means that the male approached more often than left, and female left more often than approached; thus the male was primarily responsible for maintaining proximity with the female (Hinde and Atkinson 1970). Overall, two patterns in proximity maintenance emerged. First, with only one exception, males were primarily responsible for maintaining spatial proximity with females within mixed-sex pairs. The exception was the oldest female and the younger male at Vancouver, in which the female played the primary role. Second, older whales were primarily responsible for maintaining their associations with younger belugas within same-sex pairs. The exception was the intermediate and youngest females in Vancouver, in which the youngest female played a slightly larger role in maintaining the association. On the basis of these age and sex patterns, the two similar-aged females at Point Defiance would have been predicted to have a symmetric relationship. However, one female played a much larger role in maintaining the association than did the other. The mother and calf fit the first pattern; the male calf was primarily responsible for maintaining proximity with his mother.

Figure 3.2a. The percent of time observed that each whale spent within 3 m of each other whale in its pool. Bars are arranged in descending order. All pairs of animals at each facility are shown. Facilities are: Aquarium for Wildlife Conservation (AWC), Brooklyn, NY; John G. Shedd Aquarium (JGSA), Chicago, IL; Point Defiance Zoo and Aquarium (PDZA), Tacoma, WA; and Vancouver Public Aquarium (VPA), Vancouver, British Columbia. Animal codes and sample sizes are given in Table 3.2.

Figure 3.2b. Total time that each pair of whales spent as nearest neighbours when 3 or more belugas were within 3 m of each other. All pairs of animals at the Point Defiance Zoo and Aquarium (PDZA), Tacoma, WA, and the Vancouver Public Aquarium (VPA), Vancouver, British Columbia, are shown. Bars are in same order as in Fig. 3.2a, and are plotted on the same ordinate for comparison. Animal codes and sample sizes are given in Table 3.2.
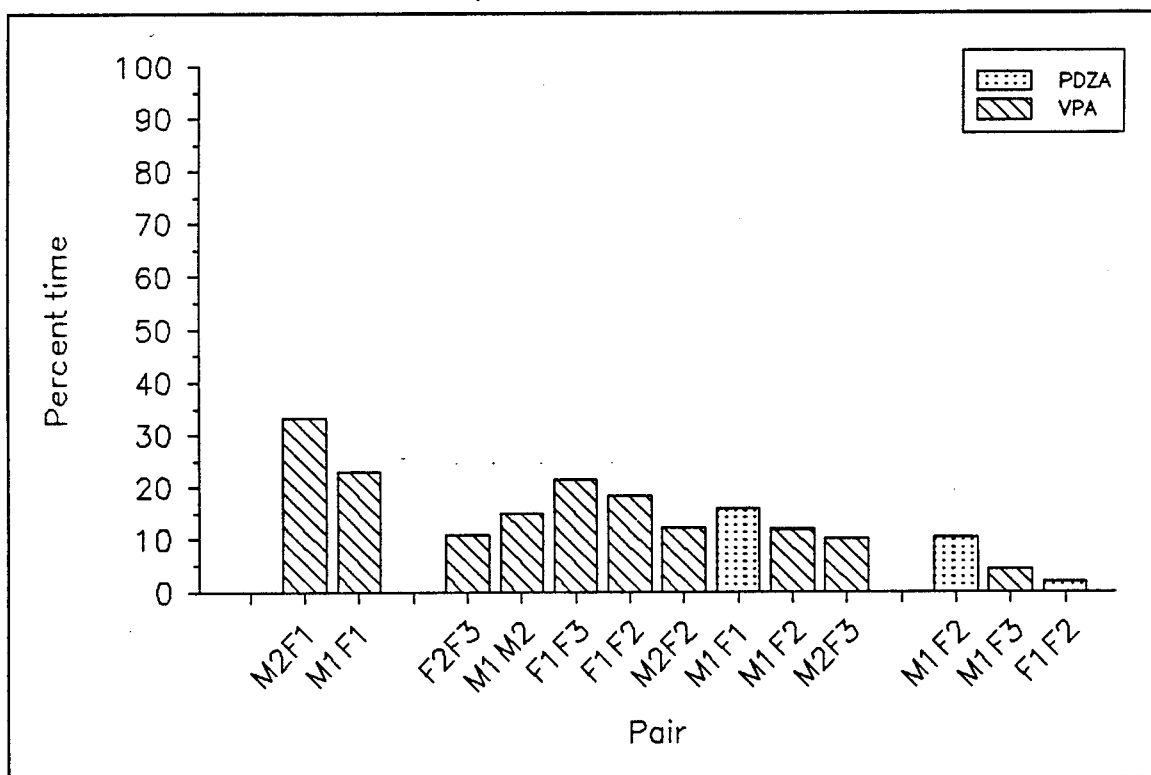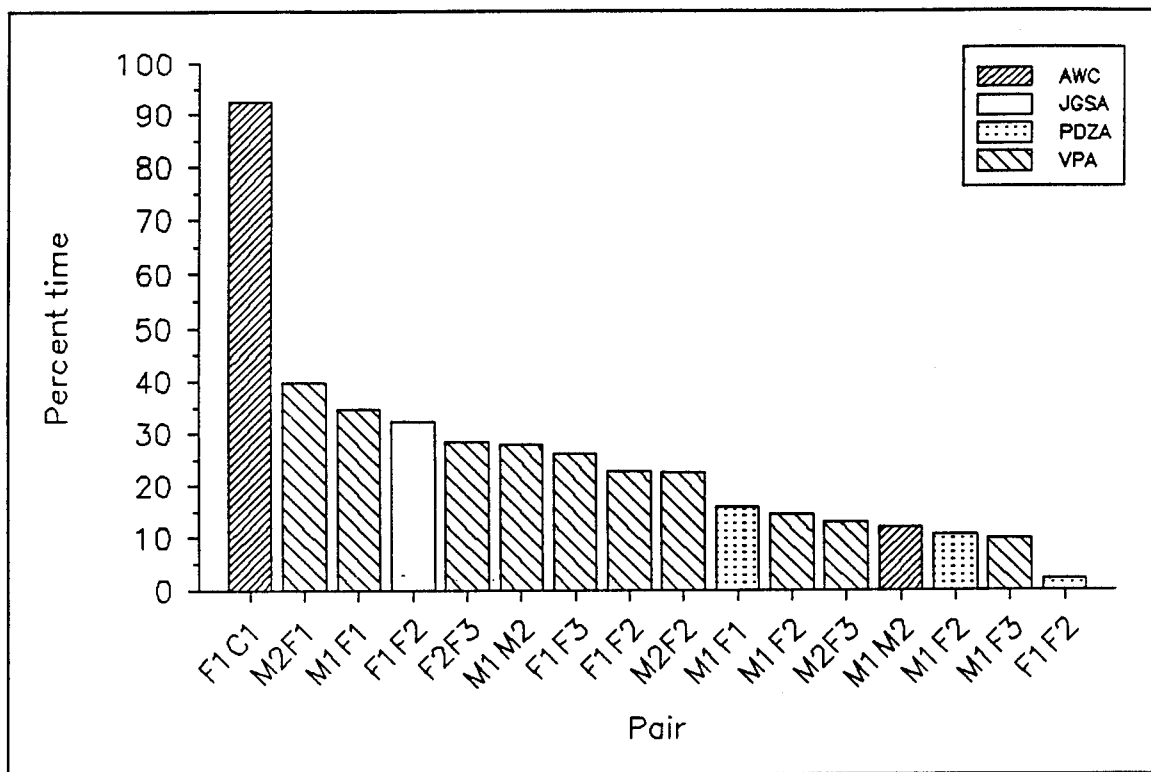
Figure 3.3. Total time that each pair of whales spent as nearest neighbours when 3 or more belugas were within 3 m of each other and animals were resting (RE) or swimming (SW). All pairs of animals at the Point Defiance Zoo and Aquarium (PDZA), Tacoma, WA and the Vancouver Public Aquarium (VPA), Vancouver, British Columbia are shown. Bars are in same order as in Fig. 3.2a. Vancouver pairs are indicated with the V- prefix, and Point Defiance pairs with the P- prefix. Animal codes and sample sizes are given in Table 3.2.

Figure 3.4. Proximity maintenance indices for all possible pairs of whales at each facility. Bars are arranged in descending order. Facilities are: Aquarium for Wildlife Conservation (AWC), Brooklyn, NY; John G. Shedd Aquarium (JGSA), Chicago, IL; Point Defiance Zoo and Aquarium (PDZA), Tacoma, WA; and Vancouver Public Aquarium (VPA), Vancouver, British Columbia. Animal codes and sample sizes are given in Table 3.2.

3.4 DISCUSSION

Selection of an association distance criterion requires balancing biological relevance and feasibility of measurement. Several researchers of odontocete social behaviour have used one body length, or a distance close to it (*e.g.* Chirighin 1987; Shane 1990; Östman 1991; Rose 1992). This measure is intuitively appealing, as it approximates the threshold at which physical contact can be accomplished by changes in body orientation and little additional travel, and is relatively easy to measure. Whales within this distance are defined as associating with the focal animal; when an animal crosses this imaginary line, an approach or leave is scored. Shorter distances can be swamped by errors in distance estimation, and longer distances can be difficult to monitor. Nonetheless, several researchers have used more than one distance criterion, and have differentiated approaches and "close" approaches (*e.g.* Taber and Thomas 1982; Smuts 1985). In the present study, an association distance criterion of 3 m, which approximates an adult beluga body length, seemed both to effectively discriminate between different types of relationships among the belugas, and provide adequate sample sizes for analysis. For the five adult belugas in New York, use of a shorter distance criterion resulted in animals being scored as alone more often than not. This did not accurately reflect the apparent patterns of association among, for example, the two oldest females. Use of a distance criterion slightly longer than a body length greatly reduced the ability of the measure to discriminate between different association patterns. The present study provides empirical support for the choice of an association distance criterion of one body length. This measure meets the requirements of biological relevance, discriminability, and practicality.

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The high association score for the mother and calf is not particularly surprising. Wild beluga calves are thought to nurse for approximately two years (Brodie 1989; Sergeant 1973), and similar close spatial associations have been noted by several authors including Brodie, who reported that "mother and calf are quite inseparable" (Brodie 1985, p. 560). The New York calf was nearly two years old at the time of this study, and although he was consuming some solid food each day, he was also nursing regularly. Much of the animals' time together was spent with the calf nursing, or nudging his mother's mammary region.

It is interesting that the dependent calf played a larger role than his mother in maintaining their spatial proximity. Hinde *et al.* (*e.g.* Hinde and Spencer-Booth 1967) examined proximity maintenance in rhesus monkey mother-infant pairs. The primary role in maintaining spatial proximity shifted from the mother, when the infant was first born, to the infant, as the infant became increasingly independent. Taber and Thomas (1982) found the same shift in the behaviour of southern right whales; in their study the transition occurred by the time the calf was approximately a year old, which roughly corresponds to the age of weaning. Chirighin (1987) used slightly different indices in her study of two captive bottlenose dolphin mother-calf pairs, but nonetheless identified the same trend. I do not have earlier data from this mother-calf pair, when the mother presumably was chiefly responsible for proximity maintenance. However, I would predict that, as the calf becomes fully weaned, he will play an increasing role in this aspect of their relationship.

Little is known of the social structure of wild belugas. Beluga groups range in size from two to hundreds and sometimes thousands of individuals (Gurevich 1980). It is believed that mature males form separate pods, while immature animals travel with adult females and their calves (Gurevich 1980; Brodie 1989). Newborn animals may be found in nursery groups with their mothers, other mother-newborn pairs, and one or more older calves (Brodie 1989). On this basis, associations between same-sex pairs of adult whales might be expected to be closer than those of mixed-sex pairs. However, the overall mean nearest neighbour scores for all animals except the mother and calf were 17% for females, 15% for males, and 15% for mixed-sex pairs. If the animals who could not form mixed-sex pairs, those in Chicago and New York, are excluded, the means for females and males are 13% and 15% respectively. These values suggest that mixed-sex and same-sex pairs had similar spatial associations.

The data from the Vancouver and Point Defiance were collected in late March and early April, which corresponds to the breeding season of at least some populations of wild belugas (Brodie 1989). Indeed sexual behaviour, including attempted mounts, was frequently observed at both facilities. The onset of the breeding season could have a significant impact on the patterns of associations between individuals. In particular, mixed-sex pairs might be expected to be more common, especially when the belugas are active. Consistent with this prediction, the mean nearest neighbour scores for mixed-sex pairs were 13% when both animals were resting, and 18% when both animals were swimming. Accordingly, the female-female mean was 14% when resting and 10% when swimming. Curiously, the male-male mean was higher when males were swimming, 18%,

vs. 9% for resting. Perhaps the males were engaging in dominance interactions when they were active.

In some primate species, higher male dominance rank correlates with increased access to reproductively receptive females in at least some populations (*e.g.* Silk 1987). One common measure of dominance is the ability of one individual to consistently supplant or displace another (Walters and Seyfarth 1987). This ability would be manifested as an asymmetry in the proximity maintenance index because the dominant animal would be responsible for most of the approaches, and the subordinate for most of the leaves. In many species, size is positively correlated with agonistic dominance rank, especially for males (Walters and Seyfarth 1987). In both Vancouver and New York, the two locations with two males, the proximity maintenance indices show that the older and larger male approached, while the younger and smaller male left.

Size may be a significant factor in determining agonistic dominance relationships among other individuals as well. Adult male belugas are significantly larger than females (Sergeant 1973; Brodie 1989). In eight of the nine adult male-female pairs, the male was primarily responsible for maintaining proximity, and in all of these pairs the male was larger than the female. Further, in the one pair in which the female was primarily responsible for maintaining proximity, that of the oldest female and the youngest male at Vancouver, she was 16 years older and much larger than he was. In total, in 11 of the 13 pairs in which there was an obvious asymmetry in the size of the animals, the larger animal was chiefly responsible for maintaining spatial proximity. One of the clear

exceptions was the mother-calf pair, which might be expected to have a relationship that was qualitatively and quantitatively different from adult relationships.

Analysis of the spatial relationships between the captive belugas has given insight into the nature of their social relationships. The methods used here provided objective, sensitive measures that elucidated interesting patterns and variability in associations across a number of different captive configurations, including two- three- and five-member groups. For example, animals did clearly prefer to spend time with particular individuals. Moreover, these preferences varied with behavioural context. However, only a coarse view of their social behaviour has been provided. Patterns of association are likely to change over time. The techniques described here could be used to quantify temporal variation in this aspect of the animals' relationships. Beyond this, a detailed quantitative analysis of their social displays is required to investigate their social interactions. The present work lays the necessary foundation for this type of approach, which would in turn facilitate quantitative analysis of the dominance relationships which may be present in the different facilities.

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CHAPTER FOUR:

AGONISTIC DOMINANCE RELATIONS

IN THREE GROUPS OF CAPTIVE BELUGAS

4.1 INTRODUCTION

Living in a social group can provide a number of advantages, including increased

protection from predators, cooperative foraging, and collective rearing of offspring (see

review in Wittenberger 1981). Yet there are also costs to group-living; group members

are often each other's most serious competitors for access to limited resources that affect

reproductive success, such as food, water, or mates (Alexander 1974; Cheney *et al.* 1987).

This competition may frequently lead to aggression. However, among many animals,

aggression often takes the form of ritualized displays between individuals, rarely

including physical violence but nonetheless leading to one animal gaining a particular

resource (Walters and Seyfarth 1987). Indeed, many species seem to use particular

signals that function as a "white flag", and convey a willingness to cease competition with

other individual conspecifics, at least temporarily (de Waal 1987). If there is a consistent

pattern between two individuals in their use of white flags, such that there is increased

predictability of the outcome of future conflicts between the two, this is often referred to

as a dominance relationship (de Waal 1987).

Sometimes, the dominance relations between pairs of individuals can be arranged

in a linear hierarchy (Hinde 1974). Schjelderup-Ebbe (1935, cited in Walters and

Seyfarth 1987) was perhaps the first to describe linear hierarchies, from his observations

of peck orders in domestic chickens. If a number of chickens are placed together in an

enclosure, there is typically a period of agonistic behaviour, with pecking and fighting among individuals. Gradually, overt aggression decreases as pairwise dominance relations are established, and these eventually become arranged into a peck order (Hinde 1974). The most dominant chicken pecks all others, the next most dominant pecks all except the most dominant, and so on.

Since Schjelderup-Ebbe's work, a voluminous body of scientific literature has been generated on dominance, particularly its form and function, in many species. In both group-living and solitary species, dominant individuals may have priority of access to limited resources. For example, octopuses are solitary animals that do not form social aggregations of any kind (Mather 1982). However, they rely on use of dens to shelter from predators. Laboratory studies have shown that dominance determines den use when dens are limited and vary in quality (Cigliano 1993). Among the social insects, subordinates (that typically do not reproduce) provide food to the dominant, reproductive females (reviewed in Wilson 1971). Among flocking birds, dominant individuals often have priority of access to high-quality food, especially during periods of food shortage (see review in Wittenberger 1981).

Dominance relationships are a central feature of many mammalian societies (Wittenberger 1981). A common benefit of being dominant, especially for males, is gaining priority of access to mates. This may occur via female preference for dominant animals, or by the ability of dominant males to hinder or prevent mating by subordinate males (Wittenberger 1981). Priority of access to limited food resources may correlate with dominance among both males and females (reviewed in Wittenberger 1981).

In general, dominance rank is a common correlate of breeding success in one or both sexes of many social species (Clutton-Brock 1988). Such a relationship has been documented or suggested in electric fish (*Hypopomus occidentalis*, Hagedorn and Zelick 1989), Bewick's swans (*Cygnus columbianus bewickii*, Scott 1988), boat-tailed grackles (*Quiscalus major*, Post 1992), capybaras (*Hydrochaeris hydrochaeris*, Herrera and Macdonald 1993), red deer (*Cervus elaphus*, Clutton-Brock *et al* 1988), and bonnet macaques (*Macaca radiata*, Samuels *et al* 1984), to name only a few species.

However, these patterns are far from universal across species, and there has been considerable debate about dominance in the scientific literature, particularly how best to measure dominance, and how or whether to develop a universal definition of dominance that is applicable to all species (*e.g.* Bernstein 1976; 1981). Rowell (1966) advocated evaluation of dominance status on the basis of approach/retreat interactions. If one animal consistently approached another, who consistently avoided the first animal, then the second animal was considered to be subordinate to the first. Approach/retreat interactions need not involve aggressive behaviour; they may consist simply of a subordinate individual avoiding a dominant animal. A key aspect of this approach to evaluating dominance is that the relationship is maintained, or expressed, primarily by the subordinate animals (Rowell 1966).

In studies of social behaviour in primates, many operational definitions of dominance have been used, but the most common measures are the direction of approach-retreat interactions as described in Rowell (1966), or the direction of aggressive and submissive behaviours in agonistic interactions (Richard 1987; Walters

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and Seyfarth 1987). For example, Hausfater (1975), in a study of reproduction in a group of yellow baboons (*Papio cynocephalus*), calculated the dominance rankings of individuals based on strict criteria of outcomes of dyadic interactions. An individual was considered to have lost an interaction if it performed submissive behaviours, but not aggressive behaviours, in response to non-submissive (*e.g.* aggressive) behaviours by another individual. If one animal consistently won interactions with another, then that pair was judged to have a stable dominance relation, with the winner dominant to the loser. Hausfater found stable dominance relations among both same-sex and mixed-sex pairs of baboons. Further, the adult females could be arranged into a linear dominance hierarchy. Adult male baboons could also be arranged into a linear hierarchy on most days of the study, but brief periods of inconsistent dominance relationships were also found. For adult males, there was a strong positive correlation between dominance and reproductive success (Hausfater 1975). Dominance has also been shown to affect reproductive success in female baboons (Altmann *et al.* 1988).

Among marine mammals, dominance and mating success have been correlated in some pinnipeds, notably northern elephant seals (*Mirounga angustirostris*, Le Boeuf and Reiter 1988). Among cetaceans, dominance has been best studied in odontocetes. Quantitative assessments of agonistic dominance relationships conducted on captive bottlenose dolphins (*Tursiops truncatus*) have revealed stable dominance relations among the individuals observed (Samuels 1988; Östman 1991; Samuels *et al.* 1991; Samuels 1992; Samuels and Gifford in prep.). In these studies, the captive environment allowed uninterrupted observations of known individuals, which greatly facilitated evaluation of dominance relations but is exceedingly difficult with free-ranging cetaceans.

Belugas (*Delphinapterus leucas*), like bottlenose dolphins and most odontocetes, are gregarious; aggregations of wild belugas often number in the tens, hundreds, or even thousands of individuals (Gurevich 1980). The mother-calf bond is known to persist for at least two years, corresponding to the average duration of lactation (Brodie 1971), but otherwise little is known of the patterns of association among free-ranging individuals. It is not known if wild belugas form long-term associations with particular individuals, as has been reported for bottlenose dolphins (Scott *et al.* 1990), sperm whales (*Physeter catodon*, Whitehead *et al.* 1991), and killer whales (*Orcinus orca*, Bigg *et al.* 1990). However, Caron and Smith (1990) identified individual belugas that returned to the same estuaries for two consecutive summers, despite hunting by local Inuit. Summer aggregations of belugas in river estuaries are considered by some researchers to be sufficiently stable to warrant designation as distinct management stocks (*e.g.* Finley *et al.* 1982). There is thus evidence of long-term site fidelity by at least some individuals. If individuals typically return to the same summering grounds, this may indicate long-term associations between individuals. If these do in fact occur, dominance may be an important aspect of the relationships between associates. If long-term associations between individuals, other than mothers and their dependent calves, are not a characteristic of beluga sociality, dominance relations may be apparent in different patterns of access to limited resources by different individuals. Limited resources for free-ranging belugas may include mates, small patches of preferred foods, and perhaps breathing holes in the ice or favoured rubbing areas.

In Chapter Two, I defined a list of directed social behaviours, including lists of aggressive and submissive behaviours, that can be used to assess dominance relations

among the captive belugas. In Chapter Three, I demonstrated unequal patterns of association between different individuals, and examined the role of each member of a pair in maintaining the pair's spatial association. The purpose of this chapter is to build upon these results, and use methods similar to those of Hausfater (1975) and Samuels (1988; 1992) to evaluate agonistic dominance relations among three groups of captive belugas.

4.2 METHODS

4.2.1 Sites and Study Animals

Behavioural data were collected from groups of belugas at three aquaria: a pair of males at the Aquarium for Wildlife Conservation, Brooklyn, New York; a male and two females at the Point Defiance Zoo and Aquarium, Tacoma, Washington; and two males and three females at the Vancouver Public Aquarium, Vancouver, British Columbia. The mother and calf in New York and the two females in Chicago were excluded from this analysis because aggressive and submissive behaviours were never or almost never seen in those pairs (Tables 2.4, and 2.5a and 2.5c).

The ages of the animals used in this analysis were presented in Table 2.2. Sexual maturity is thought to occur at approximately five years of age for females and seven to nine years for males (Stewart and Stewart 1989). Most of the study animals were therefore likely sexually mature at the time of this study. However, it is possible that the younger male in Vancouver, Imaq, was not yet fully sexually mature, as he was just seven years old at the time of this study. Certainly neither he, nor the youngest female, Aurora, were physically mature. Braham (1984) states that active breeding in belugas

does not begin until one to three years after attainment of sexual maturity. It is thus most appropriate to consider both Imaq and Aurora adolescents (*sensu* Pereira and Altmann 1985).

4.2.2 Data Collection

Data were collected during focal-animal samples (Altmann 1974). Samples were conducted during observation sessions, which were scheduled between feedings. During each sample, all occurrences of operationally-defined behaviours performed by or directed towards the focal animal were recorded. Additionally, it was occasionally possible to record occurrences of behaviours not involving the focal animal without compromising the quality of the focal-animal sample. These "non-focal", or *ad libitum*, observations were clearly denoted in the data. For each occurrence, the actor and recipient of the behaviour were noted if possible. If this determination was not possible, the behaviour was scored as "mutual". The behaviours scored, and their operational definitions and criteria for assessing directionality, are given in Table 2.3. Only occurrences that were not designated as mutual were included in this analysis. Additional details of the sampling procedure were provided in Chapter Two.

4.2.3 Dominance Scoring

Dominance scoring was done retrospectively, from the data generated during the focal-animal samples. To score winners and losers of dominance interactions, it was first necessary to define interactions. For the purposes of this analysis, an interaction was defined generally as all behaviours directed by two belugas towards each other when they were in association (within 3 m of each other, see Chapter Three). Thus an interaction

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began when two animals approached, and ended when two animals left. One exception to this general rule was made. If two belugas were within 3 m of each other, but a more than a minute passed during which the animals did not direct any of the defined behaviours towards each other, the interaction was terminated. If the pair then began to direct any of the defined behaviours towards each other again, a new interaction was begun, which continued until the animals ended their spatial association or more than one minute again elapsed without further behaviours performed. Dominance interactions were defined as those interactions in which at least one individual performed at least one submissive behaviour. Thus, I searched the data to find each occurrence of submissive behaviours, and then identified the interaction that included the submissive behaviour(s). In the results to be presented here, only dyadic interactions, involving two animals, were considered. Interactions involving three or more participants were excluded.

Aggressive and submissive behaviours were defined in Chapter Two; HIT, BITE, BITE THREAT, CLOSED-MOUTH BITE THREAT, CHARGE, SLOW CHARGE, CHASE, JAW CLAP, MOUTH OPEN, DIRECTED LOOK, HEAD JERK, FACE TO FACE, STARE, and MELON EXTENSION were considered aggressive behaviours, and FLEE, CLOSE FLEE, FLINCH, LOOK AWAY, ROLL AWAY, AVOID, and LIE PASSIVE were considered submissive. I examined each dominance interaction, and recorded the types of behaviours produced by each member of the pair: aggressive, submissive, non-agonistic (affiliative, sexual, or calf), or none. Both focal and *ad lib.* dominance interactions were examined.

Next, I analyzed the types of behaviours produced in each interaction to decide whether the interaction was decided or undecided. Following Hausfater (1975), an interaction was scored as decided only if one animal performed submissive behaviours and no aggressive behaviours in response to aggressive behaviours (or any non-submissive behaviours) by the other animal. Interactions in which both animals performed submissive behaviours, or in which one or both animals performed both aggressive and submissive behaviours, were scored as undecided. For decided interactions, the animal that performed the submissive behaviours was declared the loser, and the animal that did not perform submissive behaviours was declared the winner. The performance of non-agonistic (*e.g.* sexual or affiliative) behaviours by either or both members of the pair did not affect the scoring of dominance interactions.

Undecided interactions typically are not used to determine dominance rankings (*e.g.* Rowell 1966; Hausfater 1975; Samuels *et al.* 1984), but they can give insight into aspects of the dominance relationship of a pair of animals. For example, Walters (1980) used different types of undecided interactions to characterize the development of dominance in maturing female yellow baboons. When a stable dominance relationship between two animals reverses so that the previously subordinate animal becomes dominant, there is often an intermediate stage characterized by undecided interactions (*e.g.* Walters 1980; Pereira 1988). The proportion of dominance interactions between a pair of individuals that are undecided may be an indication of the extent that the existing relationship is established. The percentage of interactions that were undecided were calculated for each pair of belugas by dividing the number of undecided interactions by the total number of dominance interactions observed between that pair.

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The decided interactions were used to assess dominance relations in each pool. In New York, where there were only two animals, it was only possible to compare the number of times each beluga won interactions with the other to see whether there was a consistent pattern that would show that one male was dominant to the other. However, in Point Defiance and Vancouver, where there were three and five belugas respectively, it was possible to look for patterns in the pairwise dominance relations that would reveal a linear dominance hierarchy. To examine this, the numbers of wins and losses for all possible pairs of individuals were tallied, and placed in a square dominance matrix, with the rows comprising the winners, and the columns the losers. The rows and columns of the dominance matrix were arranged to minimize the number of reversals, or non-zero counts below the descending diagonal (*e.g.* Hausfater 1975; Altmann 1980; Samuels *et al.* 1984; Smuts 1985). The matrix was then examined to assess linearity of dominance relations within the pool. Separate matrices were constructed for the Point Defiance and Vancouver belugas.

The procedure just described allowed assessment of dominance relations based on the behaviours defined as aggressive and submissive. However, the list of submissive behaviours from Chapter Two included both acts which were clearly submissive, FLEE, CLOSE FLEE, and FLINCH, and acts which were placed in that category because they were more often associated with the clearly submissive acts than with behaviours of any other type. The latter submissive behaviours, consisting of LOOK AWAY, ROLL AWAY, AVOID, and LIE PASSIVE, were occasionally seen in other contexts as well. It is possible that some or all of these behaviours either are not purely submissive behaviours, or that their

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meaning depends in part on the context in which they are given. If so, then scoring such behaviours as submissive in dominance interactions may be misleading.

To counter this possibility, the dominance interactions were re-scored, counting only FLEE, CLOSE FLEE, and FLINCH as submissive behaviours. This was a more conservative criterion for scoring wins and losses because the list of submissive behaviours was restricted, and animals could not be said to have lost an interaction unless they performed one or more of these three behaviours. The same restriction was not applied to the list of aggressive behaviours. Consideration of all possible aggressive behaviours in the scoring is the most conservative criterion because animals cannot be said to have lost an interaction if they perform any aggressive behaviours. Dominance matrices were constructed with the re-tabulated wins and losses. The results generated under these criteria were compared with those produced using the full list of submissive behaviours.

4.3 RESULTS

4.3.1 Aquarium for Wildlife Conservation

Six dominance interactions were observed during the 426 minutes of observation of the two males in New York. All of these were decided, with the older male, M1, scored as the winner. In each dominance interaction, the younger male performed at least one of the clearly submissive behaviours, FLEE, CLOSE FLEE, and FLINCH. The older male thus clearly dominated the younger male.

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4.3.2 Point Defiance Zoo and Aquarium

A total of 191 dominance interactions was observed during the 1381 minutes of observation of the male and two females in Point Defiance. Of these, 16 (8.3%), were undecided. In contrast to the dominance interactions in New York, reversals, or non-zero counts below the descending diagonal of the dominance matrix, did occur in Point Defiance (Table 4.1a), but only if the less conservative measure of submission was used. When the list of submissive behaviours was reduced to FLEE, CLOSE FLEE, and FLINCH, the number of decided interactions decreased from 175 to 61, and no reversals occurred (Table 4.1b).

Regardless of the measure of submission used, the male, M1, dominated both females, and one female, F1, dominated the other F2 (Tables 4.1a-b). Thus, the pairwise dominance relations among the belugas in Point Defiance could be arranged to form a linear hierarchy, with the male as the top-ranking animal, F1 as the mid-ranking animal, and F2 as the bottom-ranking animal in the hierarchy.

Tables 4.1a-b. Dominance matrices for belugas at the Point Defiance Zoo and Aquarium, a) with all submissive behaviours and b) with only FLEE, CLOSE FLEE, and FLINCH. Within each matrix, rows and columns are ordered to reduce the number of non-zero entries in cells below the descending diagonal (see text for further details). Animal codes and sample sizes are given in Table 2.2. Behaviours are defined in Table 2.3.

Table 4.1a

Winner	Loser		
	M1	F1	F2
M1	--	34	105
F1	7	--	27
F2	1	1	--

Table 4.1b

Winner	Loser		
	M1	F1	F2
M1	--	12	30
F1	0	--	19
F2	0	0	--

4.3.3 Vancouver Public Aquarium

A total of 410 dominance interactions was observed during the 2133 minutes of observation of the two males and three females in Vancouver. These animals had the highest percentage of undecided interactions: 80, or 19.5%.

The dominance rankings of the belugas in Vancouver depended in part on the behaviours scored as submissive. Using the full list of submissive behaviours, the rank ordering from highest to lowest was the older male, the adolescent male, the oldest female, the intermediate female, and the adolescent female (Table 4.2a). This tabulation also produced many reversals; there were non-zero entries in seven of the 10 cells beneath the diagonal. Additionally, the resulting relations could not be arranged to form a linear hierarchy. F1 did not win any interactions with F3, and lost two. By this measure, F3, the adolescent female, dominated F1, the oldest female.

However, this result was not obtained when the more conservative measure was used (Table 4.2b). Restricting the list of submissive behaviours reduced the number of decided interactions from 330 to 119, and decreased the number of reversals to a total of 17 in three cells, all of which involved the younger male, M2. Using the more conservative criteria also allowed the pairwise relations to be arranged to form a linear hierarchy. Restriction of the definition of submissive behaviours also changed the relative rankings of the oldest female, F1, and the adolescent male, M2. Thus, by this measure of dominance, the dominance rankings of these animals from top to bottom, were as follows: M1, F1, M2, F2, F3.

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Tables 4.2a-b. Dominance matrices for belugas at the Vancouver Public Aquarium, a) with all submissive behaviours and b) with only FLEE, CLOSE FLEE, and FLINCH. Within each matrix, rows and columns are ordered to reduce the number of non-zero entries in cells below the descending diagonal (see text for further details). Animal codes and sample sizes are given in Table 2.2. Behaviours are defined in Table 2.3.

Table 4.2a

			Loser		
Winner	M1	M2	F1	F2	F3
M1	--	54	15	22	68
M2	4	--	21	56	42
F1	0	8	--	3	0
F2	1	19	0	--	7
F3	0	6	2	2	--

Table 4.2b

			Loser		
Winner	M1	F1	M2	F2	F3
M1	--	0	28	4	22
F1	0	--	2	0	0
M2	1	0	--	23	19
F2	0	0	13	--	4
F3	0	0	3	0	--

4.3.4 Analysis of Undecided Interactions

There were no undecided interactions in New York. In both Point Defiance and Vancouver, higher percentages of dominance interactions were undecided when the interactions involved two animals of adjacent rank, compared to interactions involving animals two animals with greater disparity in ranking. In Point Defiance, undecided interactions accounted for 16.3% of the dominance interactions between top-ranked M1 and second-ranked F1, and 9.7% of the interactions between F1 and third-ranked F2. In contrast, only 4.5% of the interactions between M1 and F2 were undecided. In Vancouver, high percentages of undecided interactions occurred between M2 and F1, and between F2 and F3 (Table 4.3); both of these were pairs of animals with adjacent dominance rankings. In contrast, top-ranked M1 had low percentages of undecided interactions with both fourth-ranked F2 and fifth-ranked F3. The other high percentages of undecided interactions all involved M2.

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Table 4.3. Percentage of dominance interactions among each pair of belugas at the Vancouver Public Aquarium that were scored as undecided (see text for details). Animals are arranged in rank ordering from Table 4.2b. Percentages for F1&F2 and F1&F3 were not calculated because the total number of dominance interactions was less than five for both these pairs. Animal codes and sample sizes are given in Table 2.2.

	M1	F1	M2	F2	F3
M1	--	6.3	21.6	8.0	0
F1		--	34.1	N/A	N/A
M2			--	27.9	20.0
F2				--	25.0
F3					--

4.4 DISCUSSION

The results presented here demonstrate pairwise agonistic dominance relations within all three of the beluga groups studied. The dominance relation between the two males in New York was clear-cut; the younger male won none of the decided interactions with the older male, and there were no undecided interactions.

Clear dominance relations were also revealed for the belugas in Point Defiance and Vancouver. However, the conservative scoring method, using the restricted list of submissive behaviours, produced the strongest asymmetries. A linear dominance hierarchy could be constructed at Point Defiance regardless of the behaviours scored as submissive, but a cleaner result was obtained under the conservative condition. In Vancouver, a linear dominance hierarchy could be produced only by using the restricted list of submissive behaviours. Use of the broad definition of submissive behaviours not only resulted in reversals in almost every cell of the dominance matrix, but also indicated

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that the adolescent female dominated the oldest female. This is unlikely to be an accurate representation of their relationship. The older female was much larger than the adolescent female, and frequently displaced her from preferred areas of the pool, such as favourite rubbing places (personal observation). Indeed, the adolescent female was often displaced by all of the other animals, and was considered by the trainers to be the bottom-ranking animal in the pool. In another behavioural study of the Vancouver belugas, Delfour (1993) suggested that the oldest female may be dominant to the two other females, but did not specifically measure dominance. I conclude that the more conservative assessment, based on the restricted list of submissive behaviours, provided a more accurate representation of the dominance relations among the animals.

Overall, a clear pattern in pairwise dominance relations emerged; larger animals dominated smaller animals. In New York, the older male was much larger than the younger male. In Point Defiance, the male was larger than both females. In Vancouver, the top-ranked older male was the largest animal in the pool, and the oldest female dominated the other females, who were both smaller than she was. Additionally, the adolescent male in Vancouver clearly dominated the smaller intermediate and adolescent females, but his relationship with the larger, oldest female was less clear. Body size is correlated with dominance status in many species, including blackbirds (*Cacicus cela*, Robinson 1986), eastern grey kangaroos (*Macropus giganteus*, Jarman and Southwell 1986), and many primates, especially for males (Walters and Seyfarth 1987). Among species that are sexually dimorphic with respect to body size, adults of the larger sex commonly dominate adults of the smaller sex (*e.g.* savanna baboons, Hausfater 1975; Florida scrub jays *Apheloma coerulescens coerulescens*, Woolfenden and Fitzpatrick 1986;

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hyaenas *Crocuta crocuta*, Smale *et al.* 1993). Fully adult male belugas are often as much as a third larger than adult females (Stewart and Stewart 1989).

Studies of dominance in yellow baboons have shown that adult males dominate adult females (Hausfater 1975; Pereira 1988). However, smaller juvenile males are often subordinate to at least some of the adult females in their social group (Pereira 1988). As the young males mature and increase in size, they dominate an increasing number of adult females, until they ultimately show the adult pattern (Pereira 1988). Similar trends occur in Japanese macaques (*Macaca fuscata*, Rostal and Eaton 1983), and in chimpanzees and gorillas (*Pan troglodytes, Gorilla gorilla*, Watts and Pusey 1993). The results of this study provide evidence of a comparable pattern for the adolescent male in Vancouver; he clearly dominated the smaller females, but not the largest female. Additionally, a large percentage of all dominance interactions involving the adolescent male were undecided, possibly indicating that his present dominance status is not well-established. However, clear evidence of this type of progression can only be provided through long-term studies, which may provide the opportunity to document increases in dominance rank as individuals mature.

Dominance, as the term is used here, describes only one aspect of the relationship within pairs of individuals. To be useful as an explanatory concept, dominance must relate to other aspects of behaviour (Hinde 1974). Thus, if the predictable directionality in agonistic interactions described as dominance is also reflected in other types of interactions, then dominance becomes a useful variable for understanding behaviour within dyads (Hinde and Datta 1981). The dominance rankings

described for the belugas in this study correlate with other aspects of the behaviour between individuals. The overall rates of aggressive and submissive behaviours between pairs of individuals correspond well to the dominance ranks insofar as predictions of dominance based on those rates agree with the present findings (see Chapter Two). Because dominance was measured considering both aggressive and submissive behaviours, the dominance assessments are not completely independent of the rates of aggressive and submissive behaviours. However, they measure different aspects of agonistic behaviour.

The ordinal dominance ranks also are reflected in the sign, and in some cases the relative magnitude, of the proximity maintenance indices (Chapter Three, Fig. 3.4). Within pairs of adults, it was the dominant animal who approached, and the subordinate who left, and the magnitude of this difference corresponded to some extent to the magnitude of the difference in their rankings for most pairs. Thus, at Point Defiance, the largest asymmetry in responsibility for proximity maintenance was for top-ranked M1 and third-ranked F2. Similarly, the animals of adjacent dominance rank in Vancouver had the lowest absolute values of the proximity maintenance index. Calculation of this index is similar to measuring dominance by the direction of approach/retreat interactions as advocated by Rowell (1966). However, the proximity maintenance index compares the total proportions of approaches and leaves by both members of a pair, whereas approach/retreat analyses are typically conducted on an interaction-by-interaction basis, and thus tend to be more sensitive to temporal variations in dominance relations.

There was no clear relationship between dominance relations and patterns of association. Some animals of adjacent dominance rank, such as F1 and F2 in Point Defiance and F2 and F3 in Vancouver, spent relatively little time in association (Fig. 3.2a). Other adjacently-ranked animals, such as M1 and F1 in Point Defiance and F1 and F3 in Vancouver, spent somewhat more time together. Adjacently-ranked F1 and M2 in Vancouver spent slightly more time together, and as each other's nearest neighbour, than did any other pair of adults (Chapter Three, Figs. 3.2a-b). It is possible that this reflected an instability in their dominance relation, which was suggested by the different rankings obtained using the two different criteria of submissive behaviour. These two animals might be spending time together because they are challenging each other's relative rank. This is to some degree supported by the relatively high rates of submissive behaviours directed by these individuals towards each other (Table 2.8b). However, M2 also directed high rates of sexual and affiliative behaviours towards F1 (Tables 2.8c-d). It is likely that no single process, such as establishment of dominance rankings, is sufficient to explain fully the relationships among any of the belugas.

Nonetheless, the results of this study have demonstrated clear dominance relations among the captive belugas, and linear dominance hierarchies in the two pools that contained more than two animals. Further study is required to determine the long-term stability of these relations. Dominance relations may change with maturational events, as suggested from observations of the younger male in Vancouver. As discussed earlier, dominance rank is correlated with breeding success in many species (Clutton-Brock 1988). It remains to be seen whether this is also true of belugas.

In this study, there were no obvious proximate causes of the observed dominance interactions; it did not appear to me that the animals were "fighting over" access to immediately available resources. When I did observe one animal apparently displacing another from a preferred resource, such as a favourite rubbing area or a position in front of a water inflow, the transitions were generally peaceful, occurring without the defined agonistic behaviours, and often not involving the animals coming within 3 m of each other. Rather, one animal left the area in question, and another approached it. My impression was that the dominance interactions I observed were "about" the dominance relations of individuals, and not about immediate access to or acquisition of a resource. Further studies, using techniques similar to those described here, may reveal the functional significance of dominance ranking to captive belugas. Dominance relations may play a role in the reproductive success of the captive belugas if they affect mating. Additional observations of the belugas during breeding season may reveal whether male dominance rank influences access to reproductively receptive females. For example, the dominant male may be able to prevent the subordinate male from mating with the females, or the females may choose to mate only with the dominant male.

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CHAPTER FIVE:

STATISTICAL ANALYSIS OF VOCALIZATIONS OF CAPTIVE BELUGAS

5.1 INTRODUCTION

Acoustic communication is an essential component of the social behaviour of many species. Human observers, seeking to describe the acoustic signals of a species or group of animals, often classify signals on the basis of aural characteristics or of visual inspection of spectrographic images. Once the classification scheme has been developed, it is possible to describe an acoustic repertoire in terms of the various types or classes of sounds. Vocal behaviour can thus be quantified by examining the frequency of occurrence of signals of each class. The frequencies of occurrence may then be correlated with social context (*e.g.* feeding, fighting) and the identity or characteristics (*e.g.* age, sex) of the vocalizing individual.

This approach can be effective if the sounds of interest exhibit clear discontinuity in one or more salient physical features. For example, Ford and Fisher (1982) recorded vocalizations of killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. The most characteristic type of vocalization consisted of pulsed calls, "the majority of which can be arranged into discrete non-overlapping categories based on their physical structure seen in spectrographic analysis and from aural impression" (Ford and Fisher 1982, p. 672). Similarly, bottlenose dolphins (*Tursiops truncatus*) produce frequency-modulated whistles that are sufficiently distinctive that human listeners can learn to distinguish the whistles of individual dolphins by ear (Caldwell *et al.* 1990). These individually distinctive whistles, called signature whistles, may comprise over 90% of the

whistles produced by an individual (Caldwell *et al.* 1990). However, both killer whales and bottlenose dolphins also produce sounds which are more variable.

In fact, many species produce sounds that exhibit nearly continuous variability in features salient to human observers. These graded signals are not easily categorized using traditional methods. A few researchers (*e.g.* Clark 1982; Hoelzel and Osborne 1986; Clark *et al.* 1987) have explored methods of acoustic categorization that depend on statistical analysis of measurements of physical features of sounds. Signal digitizers allow analog recordings of vocalizations to be converted into binary files amenable to computerized analysis. Database programs allow management and manipulation of large numbers of signals. Acoustic feature extraction programs can be used to calculate descriptive statistics for the digital files. These statistics in turn can be analyzed using multivariate techniques. These methods promote a more objective approach to the problem of signal classification than the traditional method.

Sounds are of obvious importance to most marine mammals, and most appear to use purposefully-produced sound underwater (Watkins and Wartzok 1985). Sound propagates well through seawater and may be used efficiently for both close- and long-range communication. Visual, chemical, electrical, and tactile signals are undoubtedly important for many marine species, but they are best suited to communication over relatively short distances (Watkins and Wartzok 1985).

Belugas (*Delphinapterus leucas*) are renowned for their highly vocal nature. Schevill and Lawrence (1949) were among the first to record the underwater sounds of

these animals. After listening to belugas in the Saint Lawrence River, they reported that "particularly striking is the great variety of sounds... and their rapid and apparently continuous succession" (Schevill and Lawrence 1949, p. 144). They described the belugas' sounds as "high-pitched resonant whistles and squeals, varied with ticking and clucking sounds slightly reminiscent of a string orchestra tuning up..." (Schevill and Lawrence 1949, p. 143). Hay and McClung (1976) used 30 terms to describe the sounds of belugas in Cunningham Inlet, including "snarl", "latter part of lecher's whistle", "gargling", and "burp". There is also a report of a captive beluga that produced intelligible imitations of his name, "Logosi" (Eaton 1979).

Most previous studies of beluga vocalizations have involved classifying recorded signals into various numbers of subjective categories. Categorization is typically based on a combination of aural impressions of calls, visual inspection of spectrographic representations of sounds, and measurement of a small set of salient physical characteristics, such as fundamental frequency, duration, and direction and magnitude of frequency or amplitude modulation (e.g. Fish and Mowbray 1962; Morgan 1979; Sjare and Smith 1986a; Bel'kovitch and Sh'ekotov 1990). However, depending on the nature of the vocalizations involved, the resulting classification can be highly subjective and arbitrary. Inter-observer reliability of classifications can be evaluated with techniques developed to measure reliability of human judgements (e.g. Rosenthal 1982). However, none of the papers cited here described conducting such tests. Moreover, the basis for decisions about number and membership of call types is often difficult to describe precisely; the human eye and ear are capable of integrating a complex array of features and forming "types" when discrete categories may not be reflected in the acoustic

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features. These problems often become apparent when attempts are made to compare findings between studies.

The purpose of this chapter is to use both traditional subjective classification techniques and more quantitative methods to describe the vocalizations of captive belugas. Multivariate statistical techniques will be used for quantitative evaluation of subjective categories.

5.2 METHODS

5.2.1 Sites and Study Animals

Recordings of beluga vocalizations were made at three aquaria: the Aquarium for Wildlife Conservation, Brooklyn, New York; the Point Defiance Zoo and Aquarium, Tacoma, Washington; and the Vancouver Public Aquarium, Vancouver, British Columbia. Recordings from New York were obtained in May 1991 from a group of five adult belugas (Table 2.1, 5/2/91-5/9/91). Recordings from Vancouver and Point Defiance were made in March and April 1993 from groups of five and three adult belugas respectively (Table 2.2). The animals' sounds were recorded between feedings at various times throughout the day, in conjunction with behavioural observations.

5.2.2 Sound Cut Extraction

All vocalizations were recorded underwater using hydrophones. Sounds from the New York and Point Defiance belugas were recorded using a hydrophone developed by Peter Tyack for recording dolphin whistles. These hydrophones had built-in 500 Hz or 1000 Hz high-pass filters to reduce noise, and above this, their frequency response was

flat to 25 kHz (Sayigh *et al.* 1993). The Vancouver belugas were recorded with a similar hydrophone (Offshore Acoustics, frequency response ±3 dB over 100 Hz - 10 kHz, ±6 dB over 10-22 kHz). All vocalizations were recorded on VHS videotapes with a hi-fidelity portable recorder (Panasonic model AG-6400), which had a flat frequency response from 20-20000 Hz (Sayigh *et al.* 1993). Tapes were played back on a similar machine (JVC model BR-7700U, frequency response 20-20000 Hz).

The first objective of this study was to obtain a sample of vocalizations from the recorded videotapes that was as representative as possible. In New York in 1990-1991, the five belugas were housed together during the summer months. In the winters however, the two younger animals were housed in one pool, and the three older animals in a separate pool. The animals were thus separated in late fall, and reunited in the spring. The reunions were characterized by high levels of interaction among the animals, accompanied by high rates of many different types of vocalizations. In 1991, the reunion occurred on May 1. I selected tapes recorded between May 2-9, when the level of activity had subsided somewhat, but the animals were still very vocal. There were no analogous situations in Point Defiance or Vancouver that occurred within the period of this study. For these aquaria, I arbitrarily selected focal-animal samples (Chapter Two), and located the 10-minute tape segments corresponding to these samples. I thus had a record of the non-vocal behaviour of at least some of the animals during the period in which the vocalizations were recorded.

The selected tape segments were previewed with a Kay Elemetrics Corp. DSP Sono-Graph, model 5500, and then digitized using a sampling rate of 50-70 kHz,

depending on the vocalizations involved. If necessary, signals were amplified and passed through a low-pass filter set at 20-30 kHz (Frequency Devices filter/amplifier model 9002) to prevent aliasing of the amplified signal. An FFT size of 256 points was used for all signals, providing a frequency resolution of 300-400 Hz. The digitized segments were examined using a real-time spectrographic display program (Sig, Fristrup *et al.* 1992) which allows playback of all or selected portions of the digital file. The program also incorporates a noise compensation technique which can be invoked as desired. The noise compensator facilitates visualization of faint sounds (Fristrup *et al.* 1992). Using this program, I extracted all useable vocalizations from each tape segment. Vocalizations were unusable if they were so faint that they were virtually inaudible and invisible in a spectrographic presentation (even with noise compensation), or so loud that they overloaded the recording gear. Any useable vocalization sufficiently separated from adjacent signals to allow intact extraction was saved as a separate file, or sound "cut". A minimum of ten percent of each cut consisted of background noise: five percent at the beginning of the cut, and five percent at the end. The ten percent of the cut consisting only of background noise was required for the subsequent analysis (see below).

5.2.3 Subjective Signal Categories

During the extraction process, I developed a subjective classification scheme for the vocalizations. An effort was made to create mutually exclusive and exhaustive sound categories, based on aural impressions and visual inspections of spectrograms. Each sound cut was placed into one of the categories. Each sound was also given a subjective quality rating. These ratings ranged from a score of one, for sounds of excellent quality, to a score of five, for sounds of poor quality. A rating of one was reserved for sounds

with high signal-to-noise ratios and no overlapping noise. Ratings of five were given to sounds with low signal-to-noise ratios that could just barely be detected, or had overlapping noises or other undesirable characteristics. Sound cuts with overlapping signals were additionally designated as OF if the signals overlapped in the frequency domain, OT if the signals temporally overlapped, or OTF if the signals overlapped in both the time and frequency domains (Watkins *et al.* 1992). In the results to be presented here, only sound cuts of quality one to four, with no overlapping signals, were used. Thus, the poorest quality signals were excluded, but sounds of both high and medium quality were analyzed.

5.2.4 Statistical Analyses

The digital sound cuts were processed using an acoustic feature extraction program (AcouStat, Fristrup and Watkins 1992). This program first applied a noise compensation technique to the data, that began by estimating the average noise power spectrum from the initial and terminal 5% of each sound file. A multiple of this spectrum was then subtracted from the signal, and negative values were set to zero. This technique has been tested on signals of various types and quality, and results in substantially improved quantitative classification of marine animal sounds, allowing statistical comparison of sounds recorded under differing acoustic conditions (Fristrup and Watkins in prep.).

After applying the noise compensation technique, the program calculated over 80 descriptive statistics for each vocalization. These statistics described physical characteristics of each signal, including bandwidth, intensity, duration, amplitude

modulation, frequency modulation, center frequency, and interactions among these variables (Fristrup and Watkins in prep.). A matrix consisting of the subjective classifications and AcouStat statistics for all the sound cuts was imported into a data analysis package (S-plus, StatSci Inc.). Three different multivariate analyses were performed on the statistics generated by AcouStat.

The first analysis was a linear discriminant function classification (Morrison 1976). This analysis was used to evaluate quantitatively the subjective signal categories. Each point in the transformed data from the discriminant function analysis was plotted using its subjective class label.

The second analysis was a principal components analysis (Morrison 1976). The data were first rescaled such that all measurements became zero-mean, unit standard deviation entries similar to z-scores, to prevent artifacts of the scale of measurement from influencing the covariance structure of the data (Morrison 1976). Principal components analysis allows visualization of data plotted on axes that maximize variance. This analysis was conducted to evaluate the possibility of natural categories of vocalizations that could be revealed by the AcouStat statistics, but that were not coincident with the subjective classification scheme. The results of the principal components analysis were plotted. A few points, corresponding to good exemplars of subjective sound categories, were plotted by their subjective class labels to facilitate comparison with the results of the discriminant function analysis.

The third analysis was a tree-based classification of the data. Both linear discriminant function and principal components analysis are most easily interpreted for multivariate normal data. Discriminant analysis also assumes that the populations of interest have different mean vectors but a common covariance matrix (Morrison 1976). In contrast, tree-based analysis is a very different approach. Unlike discriminant analysis, this technique accommodates heterogeneity within individual classes (Fristrup and Watkins in prep.). The analysis proceeds by binary recursive partitioning, which successively splits the data into subsets of increasing homogeneity (Clark and Pregibon 1992). Heterogeneous classes are split into more homogeneous subsets, which are ultimately depicted as terminal nodes in the tree. Thus, if the original classes were distinct and homogeneous, the number of terminal nodes in the resulting tree would equal the number of classes. However, if some or all of the original classes were heterogeneous, the number of terminal nodes may exceed the number of classes.

5.3 RESULTS

5.3.1 Subjective Signal Categories

The videotape segments yielded 1133 digital sound cuts: 298 from New York, 332 from Point Defiance, and 503 from Vancouver. A total of 17 call categories was defined (Table 5.1). Fourteen of these were mutually exclusive call types. It was also necessary to define a catch-all category, Other, for single vocalizations that did not fall into any of the other categories, and that were too rare or too intermediate in structure to merit creation of additional specific categories. Two additional catch-all categories, Series and Non-biological, were also defined (see below).

Table 5.1. The number of signals of each subjective class that were categorized, N_c, and the number that were subjected to statistical analysis, N_s, after elimination of sounds of poor quality and of assumed non-biological origin (class XX) or of mixed signal type (class SE). Definitions of signal classes are presented in the text.

Signal Class	Code	N_c	N_s
Click	CL	110	35
Jaw Clap	JC	47	38
Yelp	YE	14	13
Chirp	CH	157	97
Noisy Chirp	NC	89	64
Chirp Combination	CO	21	18
Whistle	WH	41	21
Shifting Whistle	SW	24	15
Noisy Whistle	NW	49	40
Whistle Combination	WC	13	10
Trill	TR	6	4
Buzzsaw	BZ	77	58
Scream	SC	43	34
Other	OT	279	156
Series	SE	98	0
Non-biological	XX	65	0
Total		1133	603

A break-point of 200 ms signal duration was chosen to differentiate "short" signals, such as Chirps, from "long" signals, such as Whistles. This break-point was chosen because it appeared to approximate a real discontinuity in signal durations. However, it was to some extent arbitrary, as were many decisions about class boundaries.

Definitions for each class are presented below, in approximate order of increasing signal duration. The most distinctive categories, both aurally and visually were Jaw Claps (Fig. 5.2) and Buzzsaws (Fig. 5.12). While good representatives of each of the other vocalization categories were found, intermediates between all of the classes were common. The two catch-all categories for biological (beluga) sounds, Other and Series, included signals of widely varying physical characteristics (see below). Sample spectrograms of these classes are not presented because no one signal could be said to be representative of either of these classes.

Short duration signals

Click -- A short (<50 ms) broadband pulse, usually produced in sequences (Fig. 5.1).

Jaw Clap -- An intense, impulsive sound, aurally similar to a gunshot. This was one of the two most distinctive sound types described (Fig. 5.2).

Yelp -- A noisy broadband signal with no obvious tonal qualities and pronounced sidebands (Fig. 5.3)

Chirp -- A tonal signal of duration less than 200 ms, with or without sideband structure, and usually lacking frequency modulation (Fig. 5.4).

Noisy Chirp -- Similar to a chirp, but with a broadband component present at signal onset and continuing for at least one-third of the total signal duration (Fig. 5.5).

Chirp Combination -- A chirp with a terminating broadband component, aurally similar to a yelp (Fig. 5.6).

Long duration signals

Whistle -- A continuous tonal signal of minimum 200 ms duration , with or without sideband structure, and usually lacking frequency modulation (Fig. 5.7).

Shifting Whistle -- A whistle with an abrupt shift in dominant frequency (Fig. 5.8).

Noisy Whistle -- Similar to a whistle, but with a broadband component present at signal onset and continuing for at least one-third of the total signal duration (Fig. 5.9).

Whistle Combination -- A whistle with a terminating broadband component, aurally similar to a yelp (Fig. 5.10).

Trill -- A continuous tonal signal with up-and-down frequency modulation aurally and visually evident in at least a portion of the signal (Fig. 5.11).

Buzzsaw -- An intense, raucous, burst-pulsed sound of minimum duration 200 ms, and little or no frequency modulation. This was one of the two most distinctive sound types described (Fig. 5.12).

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Scream -- An intense, noisy signal of minimum duration 200 ms, with pronounced sidebands and usually frequency-modulated. Aurally similar to a buzzsaw, but with stronger tonal qualities (Fig. 5.13).

Other signals

Other -- A category used for signals not meeting any of the above definitions. Many of the signals were intermediate in structure between two or more of the above categories. Others were sounds heard only once or twice, and thus were considered too rare to merit the development of additional categories.

Series -- A catch-all for vocalizations of different types occurring too close together to allow separation into individual sound cuts. (Series of sounds of the same type were labelled with the appropriate class code, but were differentiated from cuts of single sounds by the designation OF, reflecting the presence of sounds overlapping in the frequency domain.)

Non-biological -- I reserved this category for sounds that I considered to be likely of non-biological origin. All of these sounds were faint, broadband short-duration sounds. They may have been produced by filter pumps, and other mechanical devices (Fig. 5.14).

Figure 5.1. Waveform and noise-compensated spectrogram of a sequence of Clicks. Individual Clicks were placed in separate digital sound files whenever possible.

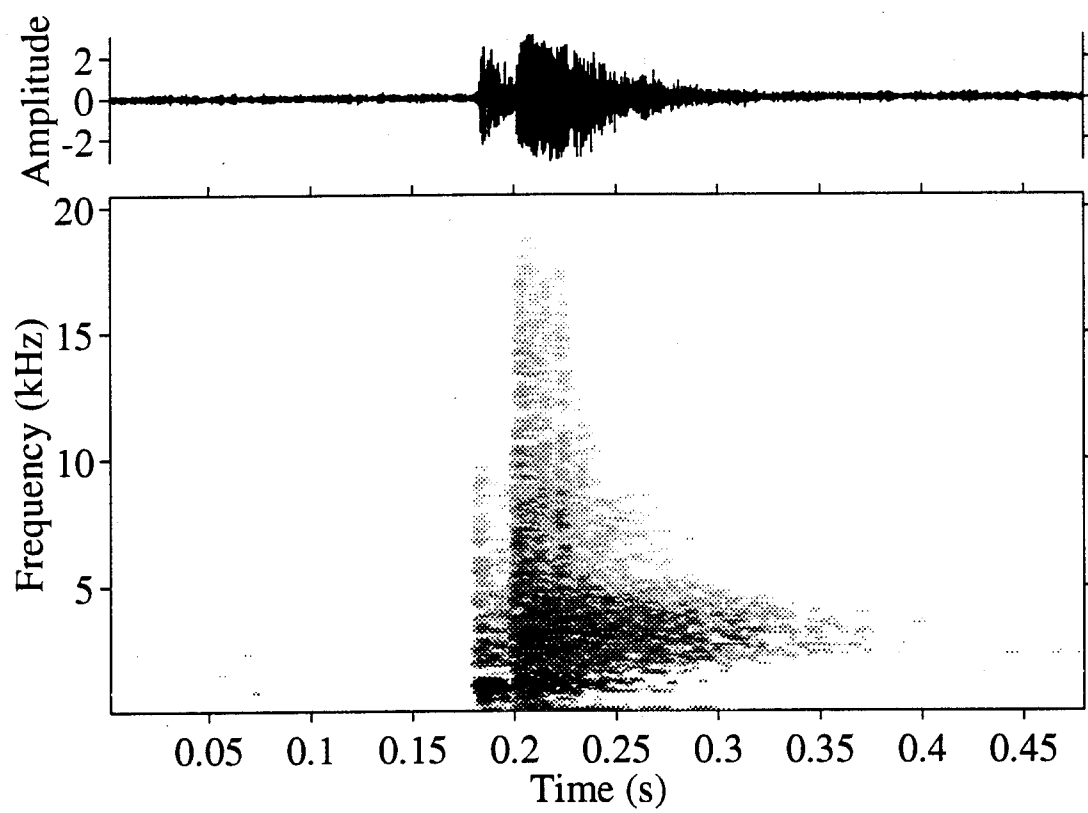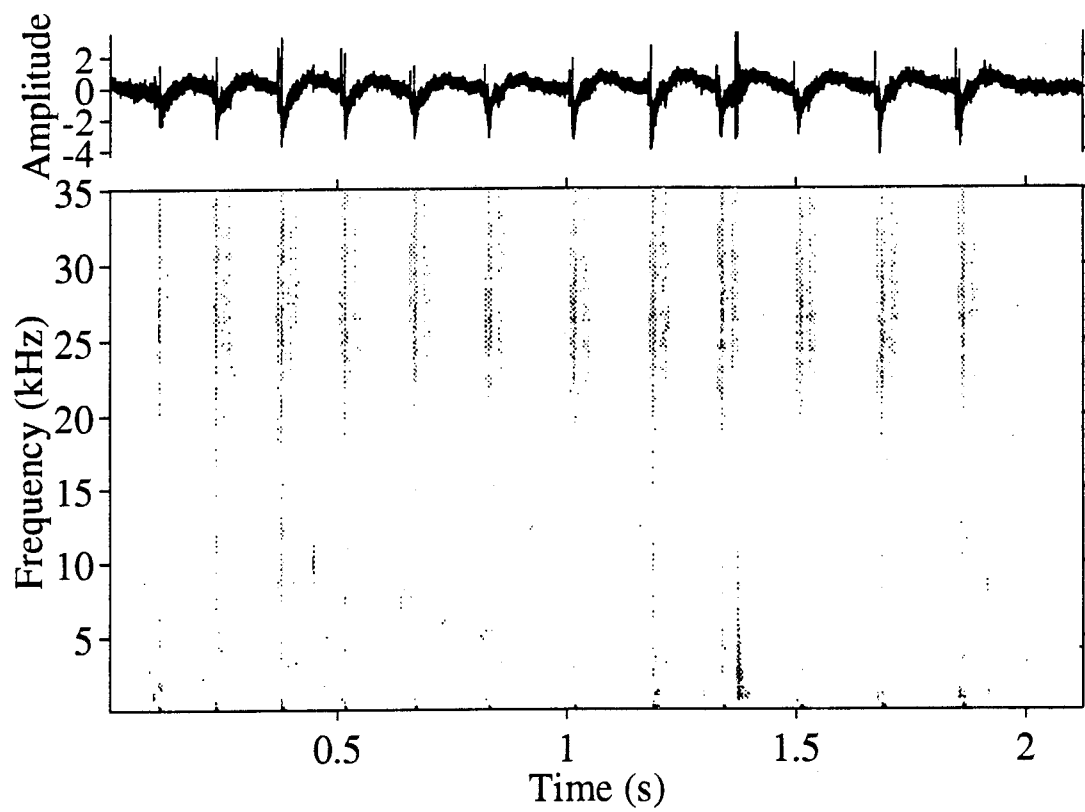Figure 5.2. Waveform and noise-compensated spectrogram of a Jaw Clap.

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Figure 5.3. Waveform and noise-compensated spectrogram of a Yelp.

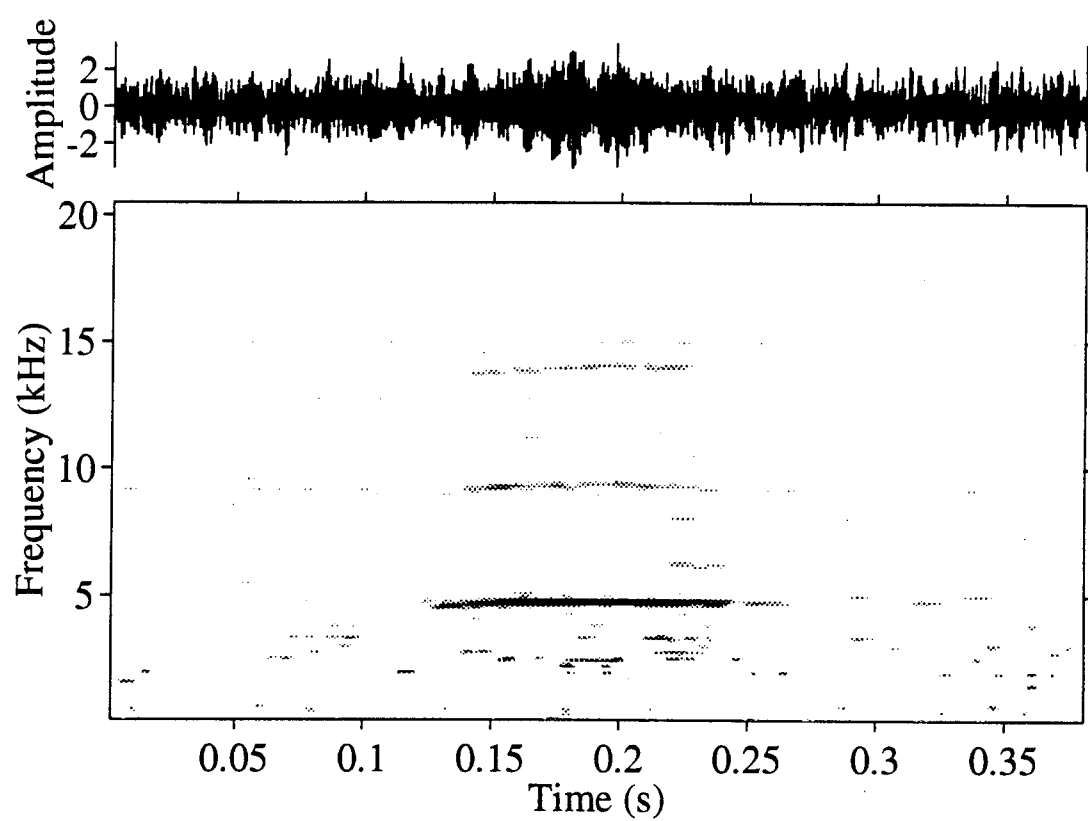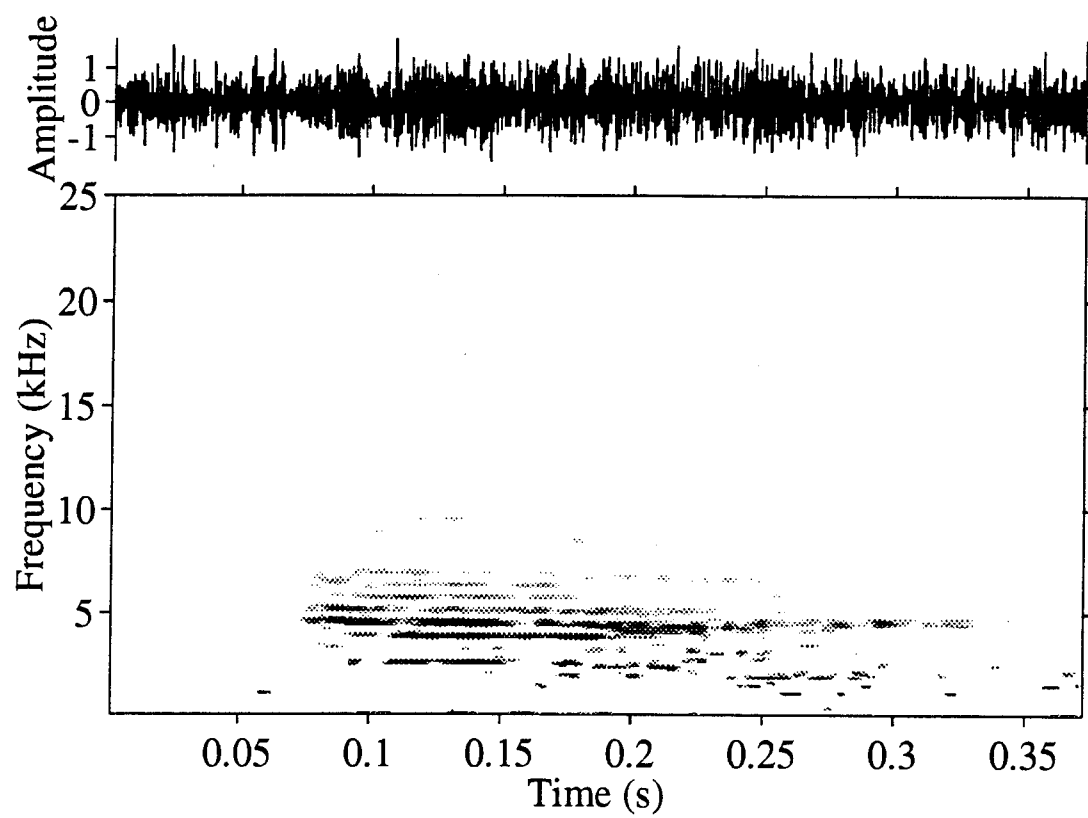Figure 5.4. Waveform and noise-compensated spectrogram of a Chirp.

Figure 5.5. Waveform and noise-compensated spectrogram of a Noisy Chirp.

Figure 5.6. Waveform and noise-compensated spectrogram of a Chirp Combination.
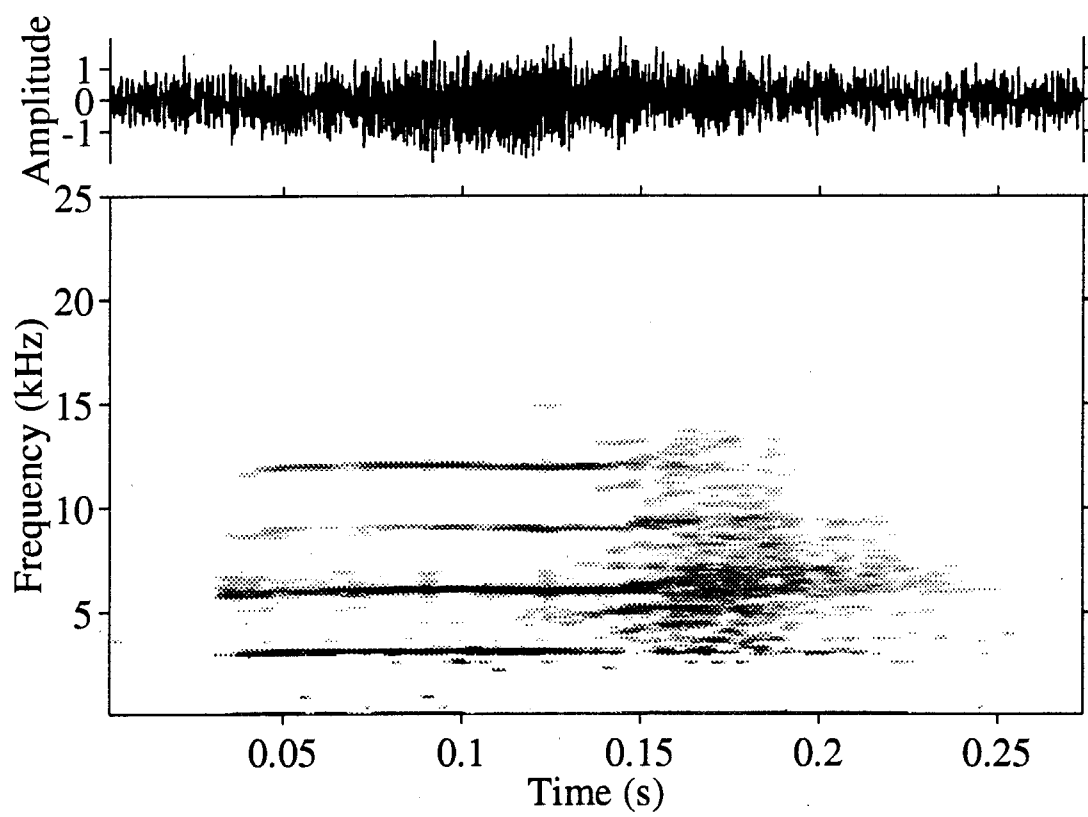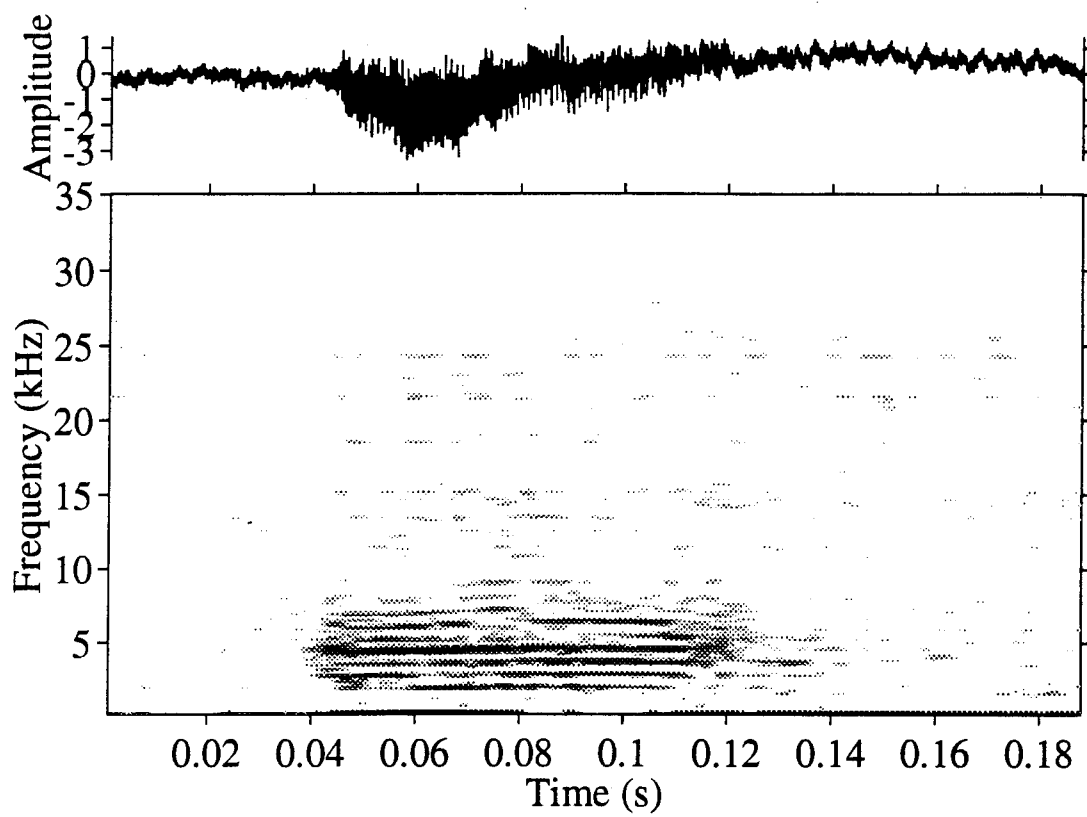
Figure 5.7. Waveform and noise-compensated spectrogram of a Whistle.
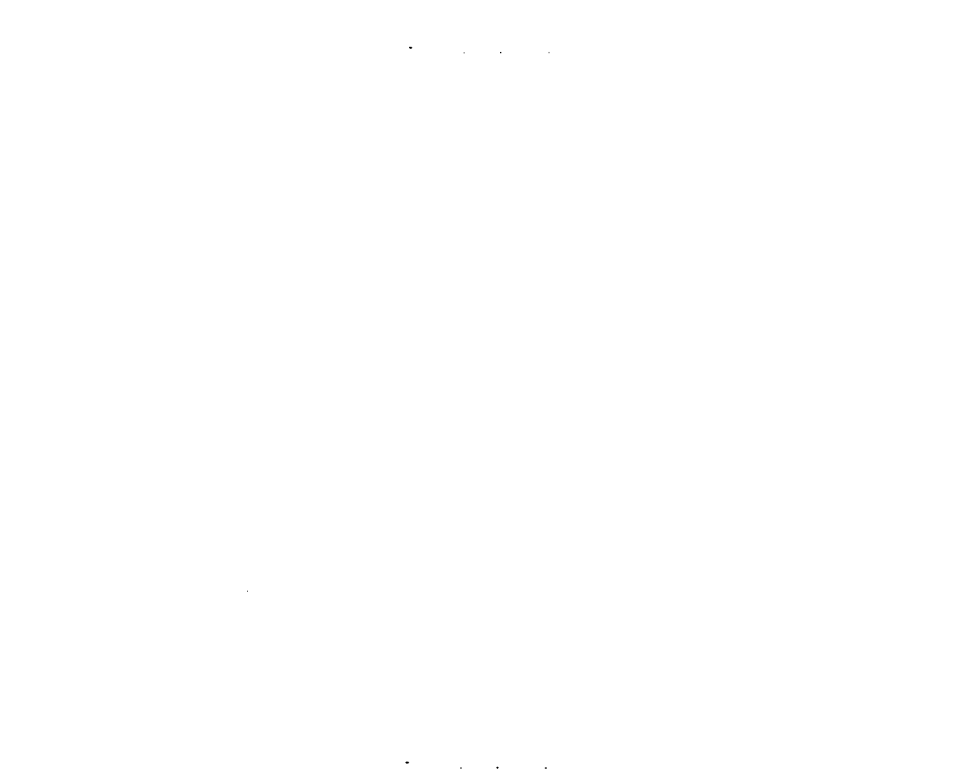
Figure 5.8. Waveform and noise-compensated spectrogram of a Shifting Whistle.

Figure 5.9. Waveform and noise-compensated spectrogram of a Noisy Whistle.

Figure 5.10. Waveform and noise-compensated spectrogram of a Whistle Combination.

Figure 5.11. Waveform and noise-compensated spectrogram of a Trill.
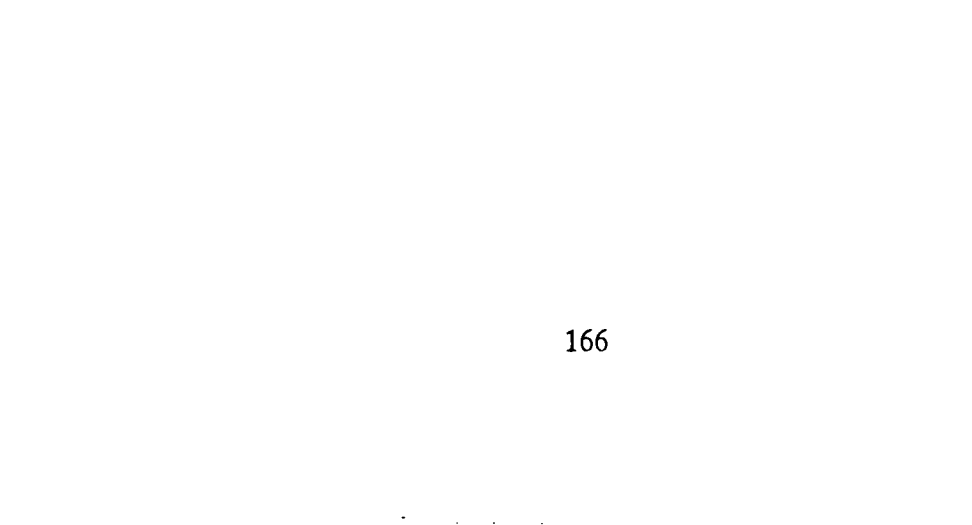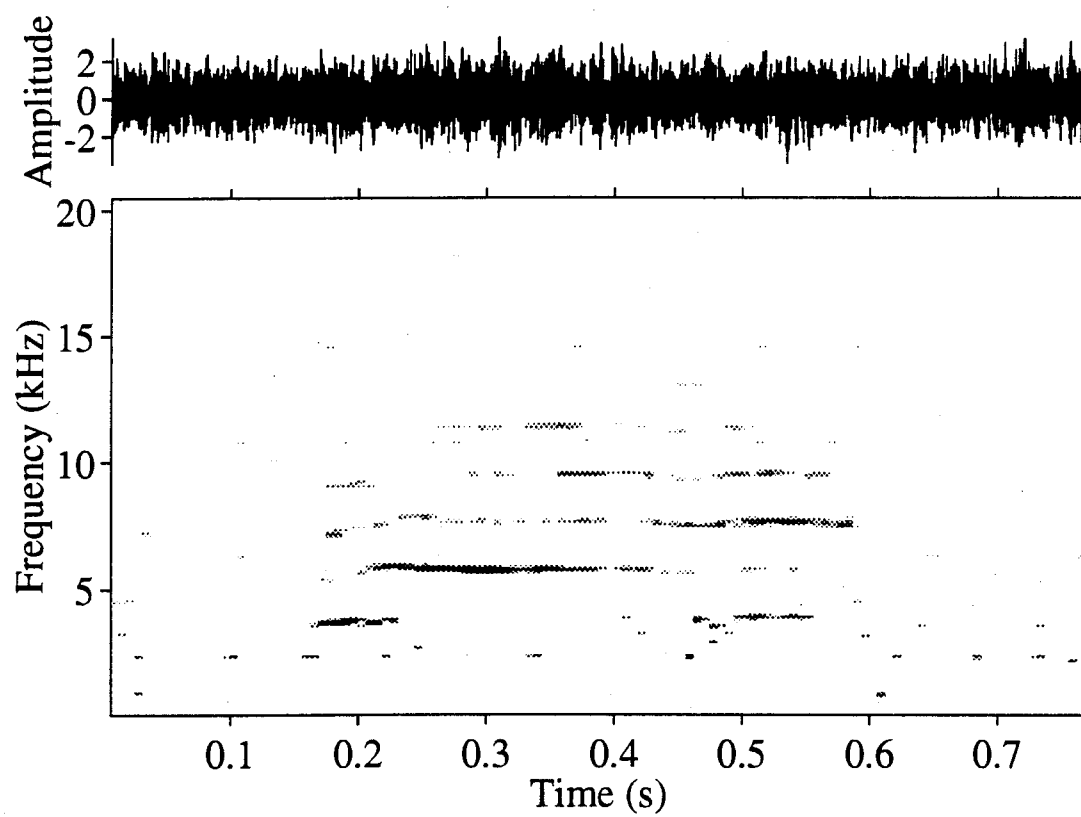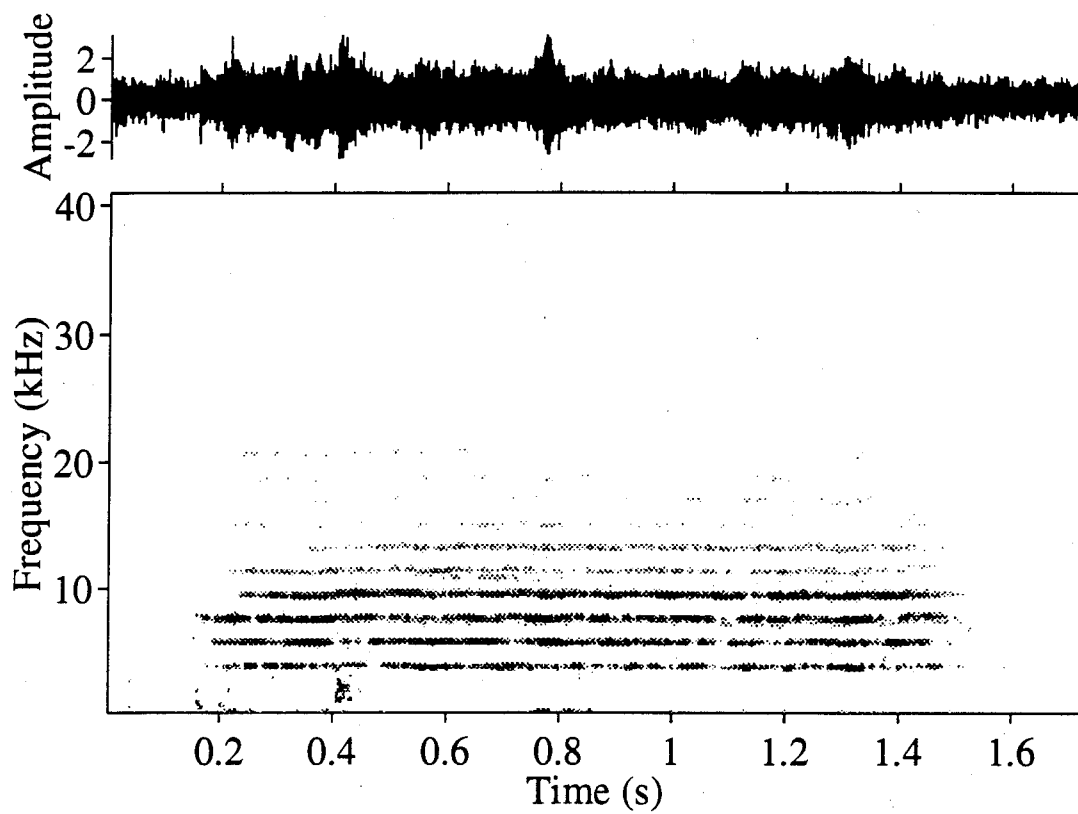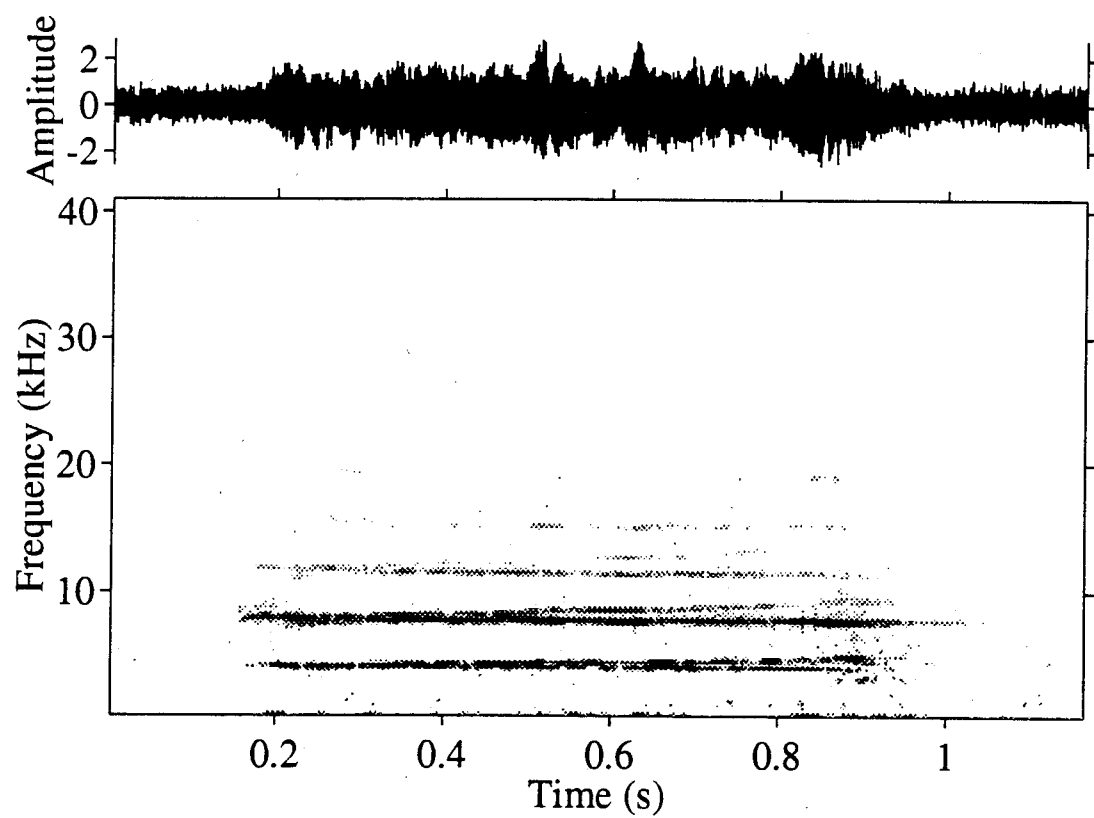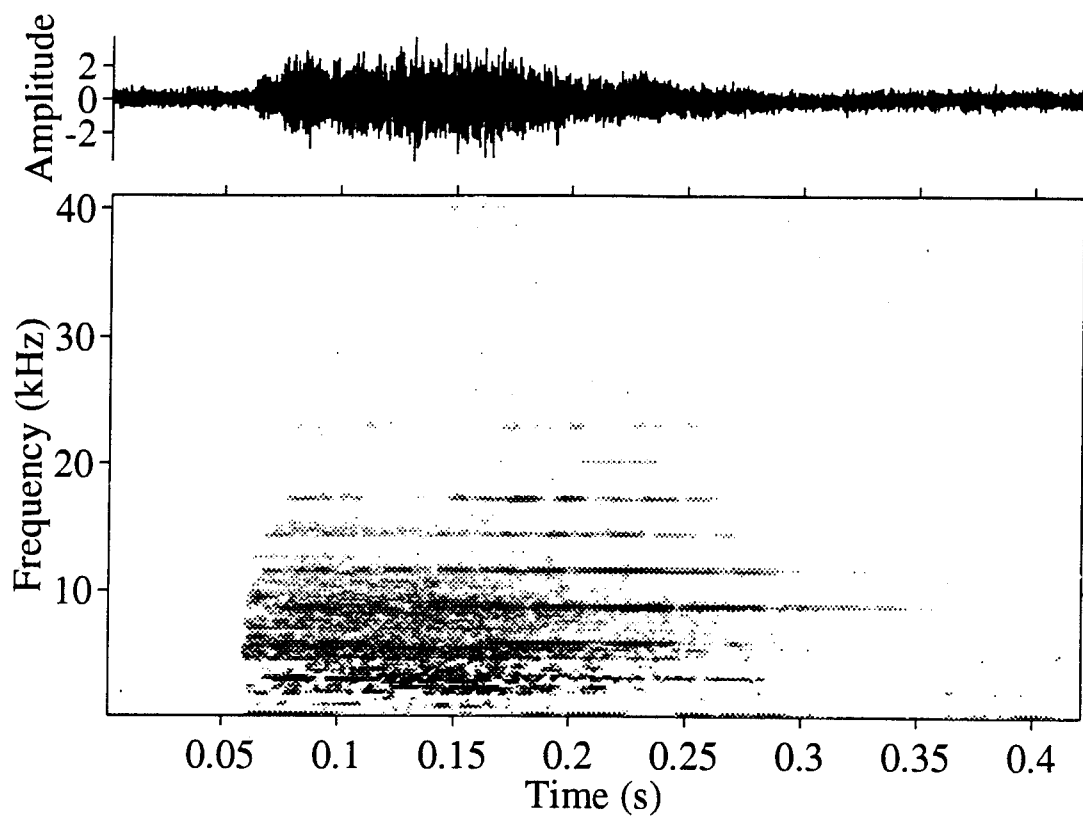
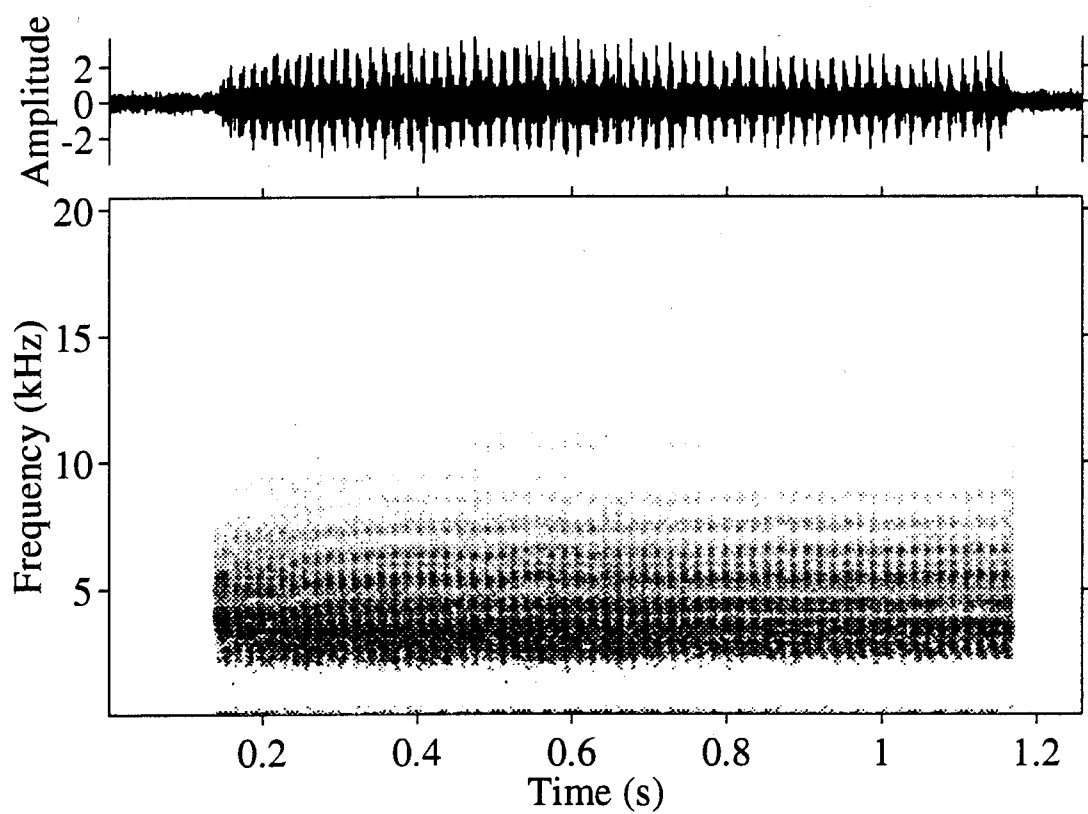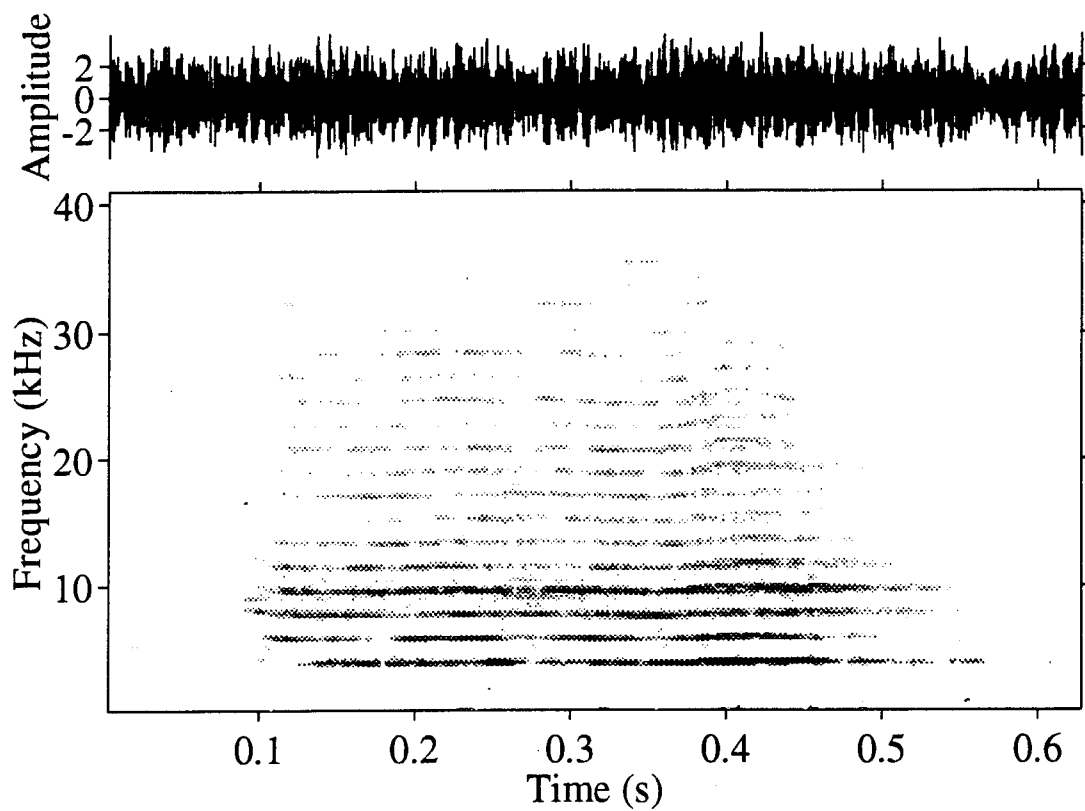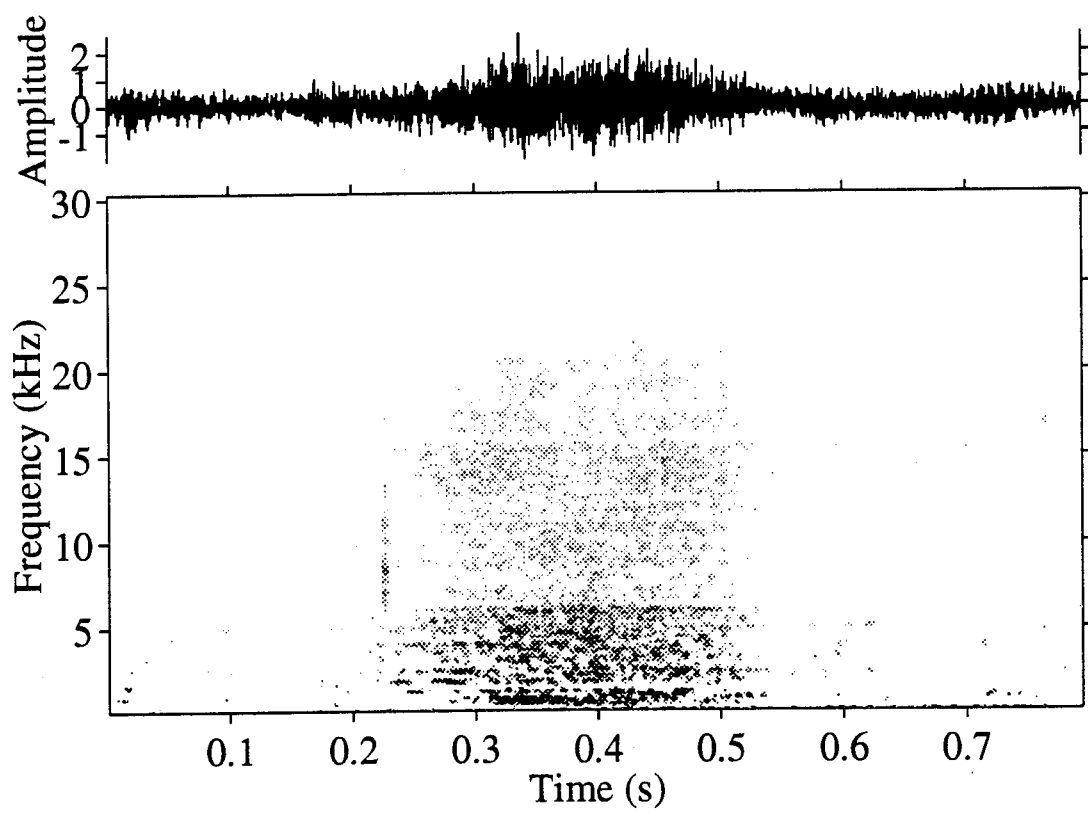Figure 5.12. Waveform and noise-compensated spectrogram of a Buzzsaw.

Figure 5.13. Waveform and noise-compensated spectrogram of a Scream.

Figure 5.14. Waveform and noise-compensated spectrogram of a presumed Non-biological sound.

5.3.2 Statistical Analyses

Two categories were excluded from the quantitative analysis. Signals classified as Non-biological were excluded because I believed these to be primarily mechanical sounds. Series were also excluded because they consisted of multiple signals of different types, rather than a single type of vocalization. After excluding the poorest quality sounds, those with a quality score of five and those with overlapping signals, 603 sounds were available for the statistical analysis: 221 from New York, 165 from Point Defiance, and 217 from Vancouver.

A plot of the first and second discriminant variables showed clustering of Buzzsaws and Jaw Claps (Fig. 5.15). The other subjective categories were not distinguished. A plot of the third and fourth discriminant variables showed some separation of Chirp Combinations and Clicks, but little differentiation of the remaining classes (Fig. 5.16).

A plot of the first two principal components showed little clustering of the data (Fig. 5.17). Sounds selected to exemplify 11 of my subjective classes clustered together, and did not align with any of the potential clusters revealed by this analysis.

The tree-based analysis correctly classified 434, or 71.9%, of the sounds to their subjective categories, in a tree with a total of 50 terminal nodes. All of the sound classes except yelps were split into two or more nodes (Fig. 5.18). Jaw Claps were split into two adjacent terminal nodes. The category Buzzsaw was split by the first partition, and eventually resulted in three nodes on one side of the tree, and one on the other.

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Examination of the variables used by the tree classifier revealed that the first division was based on a measure of the rate of frequency modulation (FMSmod, Fristrup and Watkins in prep.). The value of this statistic ranged from 0.42-1.19 (mean 0.78, n=73) for Buzzsaws on the left side of the tree, and was equal to 2.14 for all four Buzzsaws on the right side of the tree. Chirps were split into 11 terminal nodes. The category Other, which was used for all sounds that did not fit into any of the more specific categories, showed the greatest dispersion across the tree, with seven terminal nodes on each side of the tree.

5.4 DISCUSSION

Comparison of the subjective sound categories described here with those from previous studies is somewhat problematic. Schevill and Lawrence (1949, p. 143) commented on the "notorious difficulty of adequately describing unfamiliar sounds". Whistles and chirps are mentioned both by Schevill and Lawrence (1949) and by Hay and McClung (1976). However, it is difficult to know whether these sounds were similar to the Whistles and Chirps described here because there is no quantitative basis for comparison.

Figure 5.15. Plot of the first and second variables from the linear discriminant function analysis. Points are plotted with their subjective class labels. Class codes and sample sizes are given in Table 5.1.

Figure 5.16. Plot of the third and fourth variables from the linear discriminant function analysis. Points are plotted with their subjective class labels. Class codes and sample sizes are given in Table 5.1.

Figure 5.17. Plot of the first and second components from the principal components analysis of the transformed data. See text for details. Exemplars of 10 of the subjective signal classes are plotted with their class labels. Class codes and sample sizes are given in Table 5.1.

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Figure 5.18. Results of tree-based classification. The vertical distance between successive nodes is proportional to the deviance explained by the split involved. Each terminal node consists of a subset of the signals placed in one of the original subjective classes, and is labelled accordingly. Class codes and sample sizes are given in Table 5.1.

Publication of spectrograms can facilitate comparisons of sounds from different studies. Sjare and Smith (1986a) published a comprehensive description of vocalizations recorded from belugas in Cunningham Inlet. Some of their spectrograms resemble those presented here. For example, some of their pulsed calls appear similar to the Scream in Fig. 5.13, and in fact are referred to as "screamlike calls" (Sjare and Smith 1986a, Figs. 3a and 3b). Fish and Mowbray described yelps they recorded from three captive belugas, but the sample spectrogram they present (Fish and Mowbray 1962, Fig. 4) is quite different from that in Figure 5.3. Morgan also recorded sounds of captive belugas, and his spectrogram of a chirp (Morgan 1979, Fig. 1h) is superficially similar to that in Figure 5.4, and, like the Chirps defined here, is less than 200 ms in duration.

There is thus the suggestion of similarities among the vocalizations described in these studies, particularly for certain types of signals. However, most researchers of beluga vocalizations have commented on the great variability in signals produced, and this makes comparison of findings even more difficult and inconclusive, as authors struggle to capture the essence of a given category with one or two sample spectrograms. Attempting to say with certainty that the categories described here have or have not been defined (and most likely labelled differently) by other researchers is a formidable, if not impossible, task for most of the signal classes. The only signal clas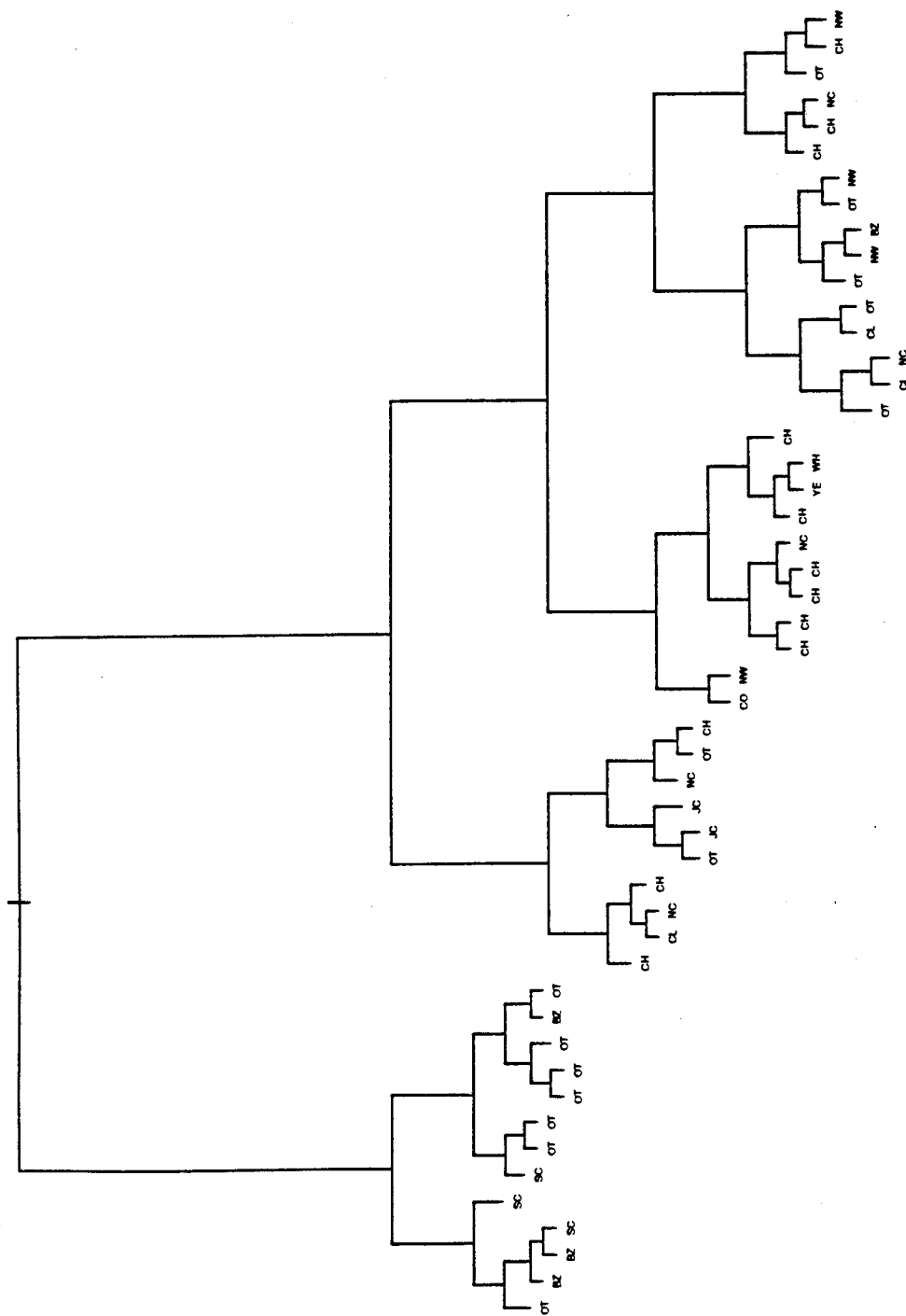s that confidently can be said to be equivalent across studies is the Jaw Clap. Jaw claps were reported by Morgan (1979) and Sjare and Smith (1986a), and may be the "bangs" referred to by Fish and Mowbray (1962), and perhaps the "sharp reports" described by Schevill and Lawrence (1949). The apparent agreement about this signal class likely stems from its loud and distinctive character, and, at least with studies of captive

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animals, from its frequent association with a rapid open and closing of the vocalizing individual's mouth.

One clear difference between the present results and those of Sjare and Smith (1986a; 1986b) is in the relative proportion of tonal signals. However, before discussing this difference, it is necessary to point out another methodological difficulty. Sjare and Smith (1986a) reserved the term "tonal" to describe sounds that contained only true harmonics that were integral multiples of the fundamental frequency. However, the term was used here to include both such "true" tonals, as well as signals that sounded tonal, but had sideband structure diagnostic of burst-pulsed or amplitude-modulated tonal signals (Watkins 1967). Sjare and Smith classified 807 of their random sample of 1243 vocalizations as tonal; in the present study, "true" tonals were very rare. For example, the Chirp in Figure 5.4 has harmonic structure indicative of a true tonal signal, while the Noisy Chirp in Figure 5.5 shows the sideband structure typical of certain types of burst-pulsed signals. Thus, Sjare and Smith relied on a physical definition of tonal, while I used aural impressions of tonality. Fish and Mowbray (1962) appear also to have used aural impression; their whistles may be true tonals, but their modulated whistle appears to be burst-pulsed.

The significance of the difference in the relative proportions of true tonals recorded from the belugas in Cunningham Inlet and the captive animals is unknown. Sjare and Smith (1986b) examined variation in the rates that different whistle types were produced under different behavioural contexts, and found that the numbers and types of whistles emitted varied little whether belugas were travelling, resting, socializing, or in an

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alarm situation. Frequency of occurrence of only one whistle type varied significantly

with changes in activity (Sjare and Smith 1986b). More pronounced effects of activity

state on vocal activity were found for other signal types, especially pulsed calls, which

were more frequent when animals were socializing. A similar relationship was reported

by Morgan (1979). Although it would be interesting to seek these kinds of effects by

correlating the occurrence of calls of each category with behavioural observations

conducted on the whales, this is problematic for at least two reasons.

First, as discussed above, traditional methods of signal description do not always

allow ready comparison of findings across studies. This can stem partly from differences

in terminology, as is the case here for use of the term "tonal", but is also due to trying to

describe complex signals with only a few parameters, and even fewer illustrative

spectrograms. Second, the results of the quantitative analyses used here reveal the

potential pitfalls arising from relying on signal categories developed subjectively by a

human observer.

While subjectively classifying the vocalizations of the captive belugas, I was struck

by the tremendous variability in the physical features of the sounds that I found salient.

By the end of the process, I felt quite uncertain about the reliability of my classification.

However, I felt confident that at least two of the classes, Jaw Claps and Buzzsaws,

represented closely related and distinctive signals. Superficially, the discriminant

function analysis supported this assessment: Jaw Claps and Buzzsaws were the classes

most clearly discriminated. This means that, given my subjective class labels and the

measurements generated by AcouStat, the discriminant function analysis most

successfully predicted group membership for Jaw Claps and Buzzsaws. The analysis was less successful at correctly predicting group membership for the other signal classes. This suggests that the majority of the subjective signal classes did not differ sufficiently on the physical attributes measured by AcouStat to allow reliable discrimination (Tabachnik and Fidell 1983). However, it was possible that the vocalizations did fall into discrete categories distinguishable by the AcouStat statistics, but that these categories did not correspond to my subjective signal classes. The principal components analysis was performed to evaluate this possibility.

Principal components analysis (PCA) examines the latent structure underlying a set of variables (Tabachnik and Fidell 1983). In this case, the many variables measured by AcouStat may reflect some smaller number of characteristics on which the sounds differed. PCA creates linear combinations of the observed variables, the AcouStat statistics, to represent latent variables, the putative signal classes. The results of the PCA of the acoustic data revealed little underlying structure; the majority of the sounds clustered together. Further, the exemplars of my subjective signal classes did not clearly align with any possible clusters. Thus, the results of the linear discriminant function analysis and the PCA essentially supported my assessment that the beluga vocalizations were too graded to allow categorization into discrete signal classes. The discriminant analysis confirmed my impression that the most distinctive signal classes were Jaw Claps and Buzzsaws.

However, the lack of evidence for discrete signal categories from these two analyses is suggestive, but not conclusive. PCA fails to resolve discrete categories if the

within-category variation is greater than the between-category separation. Linear discrimination function analysis can fail to find discrete categories if there are deviations from the assumption that each category shares a multivariate normal distribution with a common covariance matrix. Thus, even in the presence of distinguishable categories, both of these techniques can significantly under-represent the distinctiveness of categories. In contrast, tree-based classification analysis represents a very different approach. It does not require any distributional assumptions, and can accommodate heterogeneity within categories. The human eye and ear excel at perceiving patterns; discontinuities may be ignored, and complex combinations of features may be selectively attended to. Signals perceived to be similar may thus differ substantially in some physical attributes. Discriminant function analysis treats all items with the same label as belonging to a coherent group. In contrast, tree-based analysis can partition group members with the same label into multiple nodes, with each node comprising items with a higher level of homogeneity than existed within the whole group.

The results of the tree-based classification analysis agreed with those from the other two analyses, insofar as all subjective signal classes were partitioned into multiple nodes, indicating that the classes did not represent discrete categories. In accordance with my subjective impressions, Jaw Claps represented a relatively homogeneous class; they were partitioned into two adjacent nodes. However, Buzzsaws were not homogeneous. Rather, they were split by the first division of the tree. This split was accomplished by selecting the one AcouStat statistic that explained most of the heterogeneity among all signals. Thus, there are at least two subclasses of Buzzsaws that are physically very different, and these were partitioned into nodes on both halves of the

tree. Chirps, according to this analysis, represented a more homogeneous group than Buzzsaws; they remained an intact class until the second partitioning. However, they were then split repeatedly and eventually formed 11 terminal nodes. Clearly, treating Chirps and Buzzsaws, and indeed most of the subjective classes, as coherent, homogeneous categories is incorrect, at least with respect to certain physical attributes. The danger lies in assuming that these classes form distinct entities, and then basing investigations of signal meaning on that assumption.

The perils of this type of approach have been well illustrated by Hauser (1991). Much research has been conducted on the meaning of the "coo" vocalization produced by monkeys of the genus *Macaca*. Variation in acoustic morphology of coos has been associated with different social contexts (*e.g.* Lillehei and Snowdon 1978). However, Hauser (1991) examined variability in call morphology of coos produced by Rhesus macaques (*Macaca mulatta*) in three different contexts: travel, food, and female-infant affiliative interactions. His data failed to reveal significant effects of context on call structure; "acoustic variation... is so great that coos cannot be reliably classified into discrete contexts based on call morphology alone" (Hauser 1991, p. 42). Rather, call variability appeared to be explained by individual identity and putative affective state. Thus, acoustic variability in coos was attributed to two very different causes, depending on whether coos were categorized by context, or by individual.

Finally, it must be remembered that features of animal signals salient to human observers may or may not coincide with features salient to the animals themselves. Even closely related species may attend to different physical features of the same sounds.

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Psychophysical studies have demonstrated that Japanese macaques (*Macaca fuscata*) attend most closely to the relative position of the peak in the fundamental frequency of coos, whereas Rhesus macaques attend more to variation in absolute frequency (Moody and Stebbins 1989). Given this difference between two closely related species, it is unlikely that species as phylogenetically distant as humans and belugas will attend to the same acoustic features. Moreover, humans and belugas are adapted for different environments; air and seawater conduct sound differently. If the ultimate goal is to determine the meaning of an animal signal, it is important to insure that the acoustic variation described is salient to the animal of interest (Hauser 1991).

This problem becomes even more complex when potential differences in perceptual processes are taken into account. Signals may be perceived categorically by humans but continuously by animals, or vice versa. Evidence for categorical perception of signals with continuous acoustic variation has been provided experimentally for several animal species (*e.g.* chinchillas *Chinchilla laniger*, Kuhl and Miller 1975; budgerigars *Melopsittacus undulatus*, Dooling *et al.* 1987; Japanese macaques, May *et al.* 1989). To add yet another layer of complexity, researchers have suggested that some animals, like humans, perceive some acoustic features categorically, and others continuously (*e.g.* Petersen 1982; Snowdon 1982). Clearly, in the absence of information about how animals perceive their sounds, considerable caution must be exercised by human observers. Categorizing animal signals is a convenient approach for both describing repertoires and for searching for the meaning of different sounds. However, it must be remembered that human-generated signal categories may or may not reflect the true nature of the communication system at hand.

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CHAPTER SIX:

SUMMARY AND DISCUSSION

6.1 Summary of Thesis Results

The goal of this dissertation was to describe basic features of the social behaviour of captive belugas (*Delphinapterus leucas*). Of particular interest were the relations between individuals: Does the behaviour of an individual depend on whom it is interacting with? Questions like this are best approached by focusing on the behaviour of individuals, rather than groups of animals. This type of approach has long been used in investigations of the social behaviour of terrestrial animals, but has only recently begun to be employed by cetacean researchers. In the study described here, I applied this type of approach to quantify fundamental aspects of the relations between individual captive belugas. I also used quantitative methods to evaluate subjective categories of beluga vocalizations. Brief summaries of the results of each chapter of this dissertation are presented below.

6.2 Directed Social Behaviours

In Chapter Two, I identified and defined a set of directed social behaviours. Directionality of behaviours was assessed primarily through gaze cues, an approach long used in investigations of social behaviour of terrestrial animals (*e.g.* Altmann 1967). The defined behaviours were assigned to groups on the basis of my subjective impressions of their social functions. This is turn was based on temporal associations between different behaviours, which were assumed to reflect functional similarity, and on the responses of recipients to the various behaviours. Five functional groups were used: aggressive,

submissive, affiliative, sexual, and calf behaviours. Many of the defined behaviours had been reported by other beluga researchers, and similar behaviours had been described for other odontocetes.

Different individuals performed behaviours of each functional group at different rates. Generally, males (other than the dependent calf) performed all but submissive and calf behaviours at higher rates than females. Individual rates of these behaviours were also higher in larger groups; in some cases, this appeared to be a linear increase, but in others rates increased more quickly than predicted by a linear function of group size. Further, individuals not only performed behaviours at different rates, but also behaved differently depending on whom they were interacting with. These differences enabled coarse characterizations of the relations between individuals. For example, the older male in Vancouver behaved differently towards the younger male than towards the oldest female or the youngest female. The differences in the ways that particular individuals behaved towards other individuals were also used to make tentative suggestions about dominance relations between pairs of belugas.

6.3 Patterns of Association

In Chapter Three, I evaluated the effectiveness of different distance criteria in investigating patterns of association among five adult belugas. A criterion of 3 m was chosen because it fulfilled the following requirements: it discriminated between different types of relationships among the belugas, it provided adequate sample sizes for analysis of association patterns, and it was practical to use.

This distance criterion was used to examine patterns of association within several groups of belugas, to determine how much time each individual spent with other animals, and with whom each individual spent the most time. Again, differences in the behaviour of individual belugas were revealed. For example, the mother and her two-year-old calf spent almost all of their time together, while the two males in New York spent very little time together.

The relative contribution of the members of each pair of belugas to maintaining their spatial association was quantified by comparing the proportion of approaches and leaves by each pair member. A clear pattern emerged. For pairs in which there was an asymmetry in the body sizes of the pair members, the larger animal performed a higher proportion of the approaches, and the smaller whale performed a higher proportion of the leaves. It was suggested that this may reflect the dominance of larger animals over smaller animals.

6.4 Agonistic Dominance Relations

In Chapter Four, I used techniques similar to those used in studies of dominance in primates to assess the agonistic dominance relations among three groups of belugas. The assessments were based on a strict definition of winning and losing an interaction; following Hausfater (1975) an animal could not win an interaction unless it received, but did not itself perform, submissive behaviours. Examination of pairwise dominance interactions revealed clear asymmetries within all dyads analyzed. The clearest picture of these asymmetries was generated using a conservative approach to scoring interactions, restricting the behaviours scored as submissive to FLEE, CLOSE FLEE, and

FLINCH. Under the conservative scoring condition, the pairwise dominance relations in Vancouver and Point Defiance could be arranged into linear hierarchies, in which the top-ranked animal dominated all others in the pool, the second-ranked animal dominated all except the top-ranked animal, and so on.

Body size was a good predictor of dominance; in all cases, larger animals dominated smaller animals. Perhaps because of the size difference, the adult males in Vancouver and Point Defiance dominated the females in their pools. However, the adolescent male in Vancouver dominated the two females smaller than he, but not the larger female. It was suggested that this animal was in transition, essentially "working his way to the top", as is seen among some adolescent male primates (*e.g.* Pereira 1988).

The predictions about pairwise dominance relations made in Chapters Two and Three corresponded well with the quantitative assessments of dominance in this chapter. Dominant animals performed higher rates of aggressive behaviours towards subordinate animals, who responded with higher rates of submissive behaviours. Dominant animals also played the larger roles in maintaining their spatial associations with subordinates; dominants tended to approach subordinates, who tended to leave. In Vancouver and Point Defiance, the extent of this asymmetry to some extent correlated with the difference in the animals' positions in the hierarchy. Thus, agonistic dominance relations were also reflected in other aspects of the relationships between individuals. However, no clear pattern was found between dominance relations and patterns of association.

6.5 Statistical Analysis of Vocalizations

In Chapter Five, I analyzed vocalizations recorded from the captive belugas. Subjective signal categories were developed based on aural impressions and visual inspection of spectrograms. An automated acoustic feature extraction program (AcouStat, Fristrup and Watkins in prep.) was used to generate over 80 descriptive statistics for each vocalization, and these statistics were subjected to three separate analyses. Discriminant function analysis of the classified vocalizations confirmed subjective impressions that the sounds were graded and did not fall into discrete categories, with the possible exception of Jaw Claps and Buzzsaws. Principal components analysis revealed little underlying structure in the data; the majority of the sounds clustered together. Tree-based analysis showed that the subjective signal classes were comprised of signals with different physical characteristics. This was true even for Buzzsaws, which I had been confident comprised a particularly coherent and distinct signal class. These results underlined the difficulties that can arise through human attempts to categorize animal signals, particularly signals that do not exhibit clear discontinuities in physical features.

6.6 Discussion

This study has shown that it is possible to conduct continuous uninterrupted focal sampling of a cetacean using a variety of directed behaviours, in which both signaller and recipient could be identified. This technique revealed differences in the relations between pairs of animals, such as in the amount of time spent together, the relative role of partners in maintaining their association, the types of behaviours directed towards one another, and the dominance relation between the two. For the larger groups of belugas,

those in Point Defiance and Vancouver, group-level relations could be expressed in the form of linear dominance hierarchies.

At the outset of this study, the least predictable component was the application of techniques developed for use with terrestrial animals to investigation of social relationships and dominance in captive belugas. However, this worked remarkably well, and yielded clear, consistent results. Surprisingly, it was the traditional component of the thesis that raised methodological concerns. Previous studies of beluga vocalizations have involved categorizing signals on the basis of aural impressions and visual inspections of spectrograms (*e.g.* Fish and Mowbray 1962; Morgan 1979; Sjare and Smith 1986; Unzaga 1992), and I expected to encounter little difficulty doing the same thing. However, this was not the case. I had great difficulty defining signal categories and was not confident that my classifications would have passed even the most cursory test of reliability. None of the previous studies have included tests of inter-observer reliability of signal classification (Rosenthal 1982), nor had they indicated that they found such classifications problematic. I also found it difficult to compare the different beluga signals described in different studies. Additionally, my investigation of beluga vocalizations suggested few, if any, discrete categories of these signals, with Jaw Claps the one possible exception.

Similar problems have been reported from efforts to categorize vocalizations of some primate species. For example, Marler (1976) attempted to classify vocalizations recorded from chimpanzees. Although 2313 signals could be placed into discrete signal categories, there were 343 signals that were intermediate. This situation closely

resembles that described here. Marler (1976, p. 264) further stated that "higher primates exhibit an unusual emphasis upon graded signals in their vocal behaviour", and speculated on possible relationships between social organization and the discreteness of vocal repertoires. Marler (1976, p. 265) suggested that signals functioning over short distances may be less constrained towards discreteness and invariance, "both because reception will be less hindered by noise in the environment, and because of the possibility of redundant visual signalling, aiding in the accurate and reliable reception of subtle signal gradations".

Certainly the belugas in this study were communicating over short distances. And it is certainly possible that visual signals could have functioned as suggested by Marler; this study quantified the importance of visual signals, which frequently occurred concurrently with vocalizations. However, as studies of speech perception have shown, sounds that are graded may nevertheless be perceived categorically (Marler 1976). Psychophysical studies of animals of several species have demonstrated categorical perception of graded signals. For example, the coo vocalizations of Japanese macaques (*Macaca fuscata*) are graded with respect to relative position of the peak of the fundamental frequency, but nonetheless are perceived categorically by conspecifics (Petersen 1982; May *et al.* 1989). Chinchillas (*Chinchilla laniger*) perceive graded speech sounds categorically (*e.g.* Kuhl and Miller 1975). The only way to resolve whether the graded beluga signals function in a graded communication system, or are perceived categorically, is to test auditory perception in belugas.

This can be approached experimentally by training belugas to judge presented

pairs of sound stimuli as "same" or "different", and then respond by pressing a paddle or

giving some other trained response. This type of approach has been used to test

cognitive processes and perception in bottlenose dolphins (*Tursiops truncatus*, *e.g.*

Herman and Arbeit 1973; Herman and Gordon 1974) and California sea lions (*Zalophus*

californianus, *e.g.* Schusterman *et al.* 1972; Schusterman and Krieger 1986). However, a

less artificial approach that may provide insight into how belugas perceive their sounds is

to use biologically significant factors as the context within which to examine

vocalizations. As Hauser (1991) described, individual identity, affective state, and social

context can all correlate with acoustic variability in vocalizations. Among cetaceans, a

good example of this occurs with whistles of bottlenose dolphins. Not only do

individuals typically produce unique "signature whistles", but the form of these whistles

can be greatly affected by the affective state of the animal (Caldwell *et al.* 1990).

6.7 Suggestions for Future Research

While this study has provided descriptions of basic aspects of the social

behaviour, it has also raised new questions, and underlined the gaps in our knowledge of

beluga sociality. Some suggestions for future studies are outlined below.

1) One of the most obvious areas for future investigation is the temporal stability of the

patterns described here. The behavioural data analyzed in this dissertation were

collected over very short periods (*e.g.* two weeks for both Point Defiance and

Vancouver). It would be interesting to know if the patterns of association change over

time. Also, the stability of the dominance relations described here could not be

evaluated, nor could the influence of maturational events be examined. The dominance analysis conducted on the Vancouver belugas suggested that the adolescent male may be advancing up the hierarchy; further studies of these animals could confirm or refute this hypothesis. Additionally, the effect of body size on dominance relations could be further investigated by determining whether the adolescent male in Vancouver becomes dominant to the oldest female when he becomes larger than she is. Finally, further research may provide evidence regarding the biological significance of dominance to the animals.

2) Another clear need is for studies of additional captive belugas. Increasing the sample sizes would facilitate detection of patterns of behaviour corresponding to different demographic groups (*e.g.* juvenile males, mothers and calves). This may also allow distinction of differences in behaviour that are attributable to individual identity from those due to differences in physical or social environment. Such information would not only provide a more complete understanding of social relationships among captive belugas, but may also be relevant to husbandry issues, including design of captive breeding programs.

3) Many of the conclusions drawn here, including the dominance assessments, rely on my subjective interpretations of the functions of the defined behaviours. A more objective basis for these interpretations would lend greater confidence to these results. This could be achieved by comparing patterns of use of behaviours by individuals with different relationships, or by further quantification of temporal associations between behaviours.

4) The vocalizations of belugas at different captive facilities could be compared. Substantial differences in non-vocal social behaviour were found between the different groups of belugas, perhaps reflecting the differences in group sizes and compositions. The categorization scheme and analysis discussed here was designed to describe the vocalizations of all the animals, and not to test for differences between groups. However, it would be interesting to determine whether the differences in rates and types of non-vocal behaviours performed at different facilities are mirrored by similar differences in the rates and diversity of vocalizations produced.

5) Elucidation of the social functions of the vocalizations of belugas, and indeed any marine animal, is greatly hampered by the difficulty humans have in localizing underwater sound sources. Thus a human observer is usually unable to determine which animal in a group produced which sounds. Analysis of patterns of signaller and recipient is a key part of human efforts to understand animal communication systems (Tyack 1991). Development of a method to determine which beluga in a socializing group produces which sound would greatly aid our efforts to determine the social functions of vocalizations. Such a method has been developed to examine use of whistles by bottlenose dolphins (Tyack and Recchia 1991), but must be modified for application to short-duration signals, such as are frequently produced by belugas.

6) Use of biological information other than, or in addition to, individual identity of the vocalizing animal, may provide valuable reference points for investigating social functions of vocalizations. For example, linking acoustic recordings to focal-animal observations may reveal patterns in vocal behaviour that otherwise may not be apparent. This

approach would clearly be much more powerful if it were possible to correctly identify the animals producing the sounds.

7) As discussed above, there is a need to determine how belugas perceive their vocalizations, and which acoustic features they attend to. Belugas are readily trained, and should be good subjects for a psychophysical investigation of their perception of acoustic signals.

8) Finally, behavioural studies of free-ranging belugas are required to determine whether the types of relationships and interactions observed from captive belugas also occur in the wild. These questions are best approached through use of techniques similar to those described here: continuous observations of focal animals using operationally-defined behaviours. Belugas are typically found in shallow coastal waters, and their summertime estuarine habitat should facilitate this type of approach. Similar studies of bottlenose dolphins near Sarasota, Florida, and in Shark Bay, Australia, are revealing much about the sociality of animals in those communities (*e.g.* Wells 1991; Connor *et al.* 1992; Sayigh 1992; Smolker *et al.* 1992). Studies of free-ranging belugas should prove equally fruitful.

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16. Abstract (Limit: 200 words)

Focal-animal sampling techniques developed for investigating social behaviour of terrestrial animals were adapted for studying captive belugas, providing quantitative descriptions of social relationships among individuals. Five groups of captive belugas were observed, allowing a cross-sectional view of sociality in groups of diverse sizes and compositions.

Inter-individual distances were used to quantify patterns of spatial association. A set of social behaviours for which actor and recipient could be identified was defined to characterize dyadic interactions. The mother-calf pair spent more time together, and interacted more often than adults. The calf maintained proximity with his mother; larger adults generally maintained proximity with smaller adults. Among adults, larger groups performed more kinds of behaviours and interacted at higher rates than smaller groups. Within dyads, the larger whale performed more aggressive behaviours and the smaller whale more submissive behaviours. Clear dominance relations existed in three groups with larger whales dominant to smaller whales.

Vocalizations of three groups were classified subjectively, based on aural impressions and visual inspection of spectrograms, but most signals appeared graded. Statistical analyses of measured acoustic features confirmed subjective impressions that vocalizations could not be classified into discrete and homogeneous categories.

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